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Shifts in nursery habitat utilization by 0-group plaice in the western Dutch Wadden Sea

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ABSTRACT: Since the mid-1980s major changes in spatiotemporal patterns of distribution of juvenile plaice have occurred in the Wadden Sea. Large juvenile (I- and II-group) plaice have almost completely disappeared from the intertidal flats in spring and summer and are no longer found in subtidal and tidal channels in autumn, consistent with an offshore movement reported in the nearshore coastal zone. In this paper we evaluate the present functional importance of the western Wadden Sea as a nursery for young-of-the-year (0-group) plaice and the changes over time compared to the mid-1980s period by analyzing abundance, growth and distribution patterns in various intertidal, subtidal and tidal channel areas. Spatiotemporal changes in habitat use were observed compared to 1986 based on a depth-stratified sampling repeated two decades later, in 2009. Present results showed that the utilization of the western Wadden Sea has greatly changed, with changing patterns of depth distribution of the 0-group. Settlement of 0-group plaice still occurred in the intertidal, however, shortly thereafter, they moved to deeper waters. Such shift in habitat use did not seem to have affected growth rates. Overall, it seems that the western Wadden Sea can still support young-of-the-year plaice population and in spite of changes in habitat use, the functional importance of the area for this group has not been affected.

KEY WORDS: Juvenile, *Pleuronectes platessa*, Habitat use, Intertidal, Subtidal, Growth, Dynamic energy budget

1. INTRODUCTION

Many temperate estuarine and shallow coastal systems provide nurseries for early life stages of marine fishes and thus, play a key role in the context of life cycle closure in marine populations (sensu Sinclair, 1988). Such habitats are generally highly productive, providing abundant food resources as well as protection to early juveniles against predators, features which allow fish to optimize the trade-off between growth and survival (Bergman et al., 1988; Beck et al., 2001; Gibson et al., 2002). Both the capacity and quality of the nursery (Gibson, 1994; Iles & Beverton, 2000; Rijnsdorp et al., 1992; van der Veer et al., 1994, 2000) and its connectivity with the adult habitat (Beck et al., 2001; Gillanders et al., 2003) are considered to influence annual recruitment levels to adult stocks in offshore waters. The residency of juvenile fish in nursery areas is species-dependent and can range from several weeks to multiple years (Cabral & Costa, 1999; Martinho et al., 2007; Laurel et al., 2009), and the longer the permanence, the stronger the potential influence of habitat (biotic and abiotic) factors on growth and cohort survival (see review by Gibson, 1994).

Despite their vital role, shallow-water systems are sensitive habitats which, in addition to natural environmental variability are also under considerable anthropogenic pressures, e.g., overexploitation, habitat loss and alteration, pollution, and climate change (Lotze et al., 2006; Le Pape et al., 2007; Thrush et al., 2008). The influence of anthropogenic disturbances, including human-induced climate change, on the quality of coastal and estuarine habitats and its fish assemblages has been widely reported (Johnson et al., 1998; Jackson et al., 2001; Thrush et al., 2008; Tulp et al., 2008; van der Veer et al., 2015). Climate-induced temperature change, for instance, has been suggested as one of the main driving forces eliciting changes in species distribution and abundance in two common European flatfish species (plaice *Pleuronectes platessa* and sole *Solea solea*) in the North Sea owing to effects in the quality (value for growth) and/or quantity (area) of their nursery habitat (Rijnsdorp et al., 2009; Teal et al., 2012).

For North Sea plaice, the Wadden Sea has been considered the main nursery ground (Zijlstra, 1972). Studies in the western Dutch Wadden Sea helped to elucidate patterns of habitat use by juvenile plaice (Zijlstra, 1972; Kuipers, 1973, 1975, 1977; de Vlas, 1979) and to evaluate plaice population dynamics in relation to variation in habitat quality (van der Veer et al., 1990; Karikiri et al., 1991; van der Veer & Witte 1993; van der Veer et al., 2010). It was established that plaice settlement is mainly restricted to tidal flat areas (Zijlstra et al., 1982; van der Veer & Bergman, 1986) and that 0-group plaice remain in this primary nursery habitat until autumn, before moving to deeper waters offshore as suggested by increasing densities in coastal waters (> 3 m depth) (Zijlstra et al., 1982; van der Veer et al., 1990). Juvenile plaice return the next two years in spring

(respectively as I- and II-group), and leave the area altogether at the end of their third year of life (Kuipers, 1977; Rijnsdorp & van Beek, 1991) joining the adult population in the North Sea.

However, spatial distribution of juvenile plaice has changed over time. In the 1980s and 1990s, large juvenile plaice in the southern North Sea gradually moved to deeper water earlier in life (van Keeken et al., 2007) and this offshore shift seems to have continued in recent years (Poos et al., 2013). Similar shifts in spatiotemporal distribution were also observed in the inshore waters of the western Wadden Sea: large juvenile (I- and II-group) plaice have almost completely disappeared from the tidal flats in spring and summer (van der Veer et al., 2011) and strongly declined in abundance in deeper parts (> 2 m depth) of the area in autumn (Tulp et al., 2008). Abundance of young-of-the-year (0-group) plaice inside the Wadden Sea, has also declined over the same period as suggested by the long term trend in fyke catches at the entrance of the Dutch Wadden Sea (van der Veer et al., 2011; 2015). These observations have led to the postulation that the role of the western Wadden Sea as juvenile plaice nursery might have declined (van der Veer et al., 2011; 2015). Although these studies have shown unequivocal long-term shifts in juvenile plaice abundance and/or spatial distribution, their lack of simultaneous focus on spatial (restricted to the Balgzand tidal flat area, van der Veer et al., 2011) and temporal (restricted to autumn, Tulp et al., 2008) scales hampers the possibility of examining in more detail the fine-scale dynamics of putative habitat shifts. Especially in the case of 0-group plaice, it is unclear whether the declining trends in the intertidal are caused by redistribution to alternative habitats in deeper inshore areas.

Whether such a habitat shift has occurred over the years can be investigated by comparing the relative importance of different habitat types (tidal flats, subtidal habitat and channels) in the past, when the nursery function of the Wadden Sea was still intact, with the present day situation. A number of different intertidal, subtidal areas and channels in the western Dutch Wadden Sea were extensively studied in the late 1980s (results partly published in van der Veer & Witte, 1993). Therefore, this extensive depth-stratified survey was repeated in 2009 and the hypothesis that a shift in habitats within main nursery areas had occurred was tested by comparing the spatial and temporal patterns in distribution and abundance of 0-group plaice. Habitat quality was investigated by evaluating growth conditions in the various habitats. Results are discussed in relation to the main factors (e.g. temperature, food availability) that potentially affect the quality of nursery habitats used by plaice (Teal et al., 2012). Previous diet studies in various nursery areas have shown that juvenile plaice can be considered as opportunistic omnivorous benthic feeders (e.g. Edwards & Steele, 1968; Kuipers, 1977; de Vlas, 1979; Poxton et al., 1983; Pihl, 1985; van der Veer & Witte, 1993). Therefore, food availability for 0-group

plaice was not based on detailed, time consuming stomach content analysis, but on estimates of potential available benthic prey biomass (c.f. van der Veer et al., 2011).

2. MATERIAL AND METHODS

2.1. Study area

Sampling stations were selected in 1986 to cover a wide range of benthic trophic conditions for juvenile plaice to allow evaluating relationships between potential food resources and plaice growth. The selection was based on *a priori* information from earlier studies on macrozoobenthic biomass (Beukema, 1989). Sampling was conducted at 18 sites located in the western part of the Dutch Wadden Sea (Fig. 1), monthly from January until December 1986, and repeated, on a nearly monthly basis from March to late October, in 2009. Sampling procedures in the two periods were identical except for slight changes in the position of a few sampling stations which had to be reallocated in relation to 1986 due to changing geomorphology of the area. Stations were distributed along different depth strata, hereafter referred to as nominal habitat types: intertidal (areas with drained tidal flats at lower low water springs, LLWS); subtidal (area between LLWS and LLWS - 5 m); and tidal channels (areas deeper than 5 m below LLWS) (Fig. 1).

2.2. Sampling

Sampling was performed over 3-4 days at daytime and restricted to a period of 3 h around high tide. This was intended to minimize the potential bias caused by exchange between intertidal and sublittoral areas as during this tidal phase, juvenile plaice in the tidal flats was found to exhibit a relatively random and stable distribution (Kuipers, 1977). Intertidal stations were sampled with a 2-m beam trawl (5-mm mesh stretched in codend, 1 tickler chain) towed from a rubber dinghy powered by an outboard motor at a constant speed of 30 m min^{-1}. At each station 2-3 replicate hauls of about 100 m each were conducted. In subtidal and channel stations, fishing was carried out with RV *Navicula* – a 20m, low draft vessel equipped with a stern-mounted gantry – with a 3-m beam trawl (10-mm mesh in codend, 1 tickler chain). Depending on the size of the area, 2-3 replicate hauls were done in subtidal stations and 1 or 2 in the tidal channels. In all cases the total distance covered at each station, from all tows combined, was on average 500 m. The geographic position of the hauls (start and end) was recorded using a GPS and used to calculate distance towed and ultimately, the swept area per trawl (3 m beam trawl). For the 2 m beam trawl, the length of the trawls was assessed with a meter-wheel fitted

outside the trawl. Fish catches were sorted alive on board and all plaice were counted and measured to the nearest mm total length (TL).

At each station, bottom temperature data were collected after trawling with a handheld conductivity meter. In 2009, the vessel's conductivity-temperature-depth (CTD) probe was used for temperature measurements in subtidal and channel stations, but, due to technical problems these data could not fully be recovered. Therefore, to evaluate temperature conditions in the different habitats in 2009, data were reconstructed based on results from three-dimensional simulations carried out with the General Estuarine Transport Model (GETM), using realistic bathymetry and environmental forcing variables for the Dutch Wadden Sea (see PACE project at http://www.nioz.nl/pace). The numerical domain has a 200 m resolution in the horizontal and 30 vertical layers and hence, included all sampling stations. Each fish sampling station was linked to a horizontal and vertical grid cell based on spatial coordinates and depth. The results for the modelled temperatures in each grid cell were saved with a temporal resolution of 30 min and from these, daily means were obtained. The performance of the model relative to temperature variability from several observational datasets for 2009 and 2010 demonstrated the model's ability to realistically simulate the hydrodynamics of the western Dutch Wadden Sea (Duran-Matute et al., 2014). Temperature differences in 1986 and 2009 were evaluated through comparison of field records taken at intertidal stations together with data from a temperature time series consisting of continuous measurements at a fixed station (NIOZ jetty) located in the Marsdiep tidal inlet, just off the southern coast of the island of Texel. This time series was described and analysed by van Aken (2008).

In both 1986 and 2009 a benthic survey was carried out at all sampling stations. For the benthic survey carried out in autumn 1986 see van der Veer & Witte (1993). In 2009, similar data was gathered but from different sources: for intertidal stations, data was obtained from a sampling program (SIBES - Synoptic Intertidal Benthic Survey) consisting of a regularly (500 m) spaced grid over the entire intertidal Dutch Wadden Sea, from July to early October (for detailed methods see Bijleveld et al., 2012 and Compton et al., 2013). From the entire grid, all points within a maximum of 500 m from stations trawled for plaice were selected. At each site, one core with a surface area of 0.017 m^2 to was taken to a depth of about 25 cm, sieved *in loco* and organisms retained were stored in the freezer (bivalves) or in a 4% formaldehyde solution (remaining macroinvertebrates) (Compton et al., 2013). Subtidal and tidal channel stations were sampled in a similar way as in 1986 using a 0.06 m^2 box core during November 2009. At each station, 5-15 samples of at least 15 cm depth were collected. Samples were sieved *in loco* through a 1-mm mesh sieve and all organisms retained were stored on a 4% formalin-seawater buffered solution and taken to the laboratory for further identification and counting. After identification and counting, for each species, biomass (g m^{-2}) was determined and expressed as ash-free

dry mass (AFDM) calculated as the weight loss of the dried remains (60°C for 48 h) during burning (560°C for 5 h). Average benthic biomass (g AFDM m^{-2}) was then calculated for each fish station.

Potential benthic food biomass for 0-group plaice was estimated following van der Veer et al. (2011) by summing the biomass of potential whole prey items and of regenerating body parts (bivalve siphons, polychaete tips) from the benthic surveys. For whole polychaetes and bivalve spat the total biomass was taken; for adult bivalves only 3% of their biomass was considered representing the mass of their siphons; and, for the polychaete *Arenicola marina*, 15% of their body mass was taken corresponding to the biomass of their tail tips.

2.3. Data analysis

Juvenile plaice were separated into age groups based on their length–frequency distribution. In those cases where size distributions overlapped or were close together (mostly in 1986 due to the presence of I- and II- group plaice), sagittal otoliths were routinely checked for the presence of annual rings by eye. Numbers caught were first corrected for size-selective mesh and catch efficiency according to Kuipers (1975) and Dapper (1978) for the 2-m beam trawl, and after Bergman et al. (1989) for the 3-m beam trawl, and then converted to densities (ind. [10^3 m^2]$^{-1}$) using the total swept area in each station (see above). For each station, the arithmetic mean plaice abundance and mean length were estimated and used as indices of population density and size over the year. Growth rates (cm d^{-1}) for 0-group plaice were estimated based on changes in mean size between 2 successive sampling dates. The median depth distribution of 0-group plaice was calculated for all sampling dates to analyse seasonal changes in distribution. This procedure was identical for both the 1986 and 2009 surveys. To evaluate the influence of food conditions on 0-group plaice growth, the relationship between both was plotted for all stations.

Growth conditions in the various habitats were evaluated by comparing observed field growth rates with estimated maximum potential growth rates established with a Dynamic Energy Budget (DEB) model (Kooijman, 2010). The DEB model quantifies energy allocation to growth, maintenance and reproduction as a function of the physiological state of the organism (size, amount of stored energy) and forcing environmental variables (water temperature, food availability). A thorough description of the standard DEB model and relevant equations for plaice is given in van der Veer et al. (2010; Eqs. 1−3), model parameters were taken from van der Veer et al. (2001, 2009, 2010) and Freitas et al. (2010), and the full procedure is described in Freitas et al. (2012). In a rather constant environment (see Kooijman, 2010), the model equations describing the dynamics of the

state variables (reserve, structure and reproductive buffer) simplify greatly and in case of growth, become mathematically equivalent to the Von Bertalanffy growth model (Kooijman, 2010). We make use of these model properties to predict expected growth rates of juvenile plaice at each station using the prevailing temperature conditions and maximum (*ad libitum*) food conditions.

Growth simulations were run with Octave (v.3.2.4) for each time step between first and subsequent sampling date as done in the estimation of field growth rates. Input temperature was the daily average of water temperature obtained from the numerical simulations of the hydrodynamic model (see above). For the 1986 survey, similar analyses were conducted but, in this case, input temperature was interpolated from monthly field measurements using a spline function. The fraction of maximum growth realized by juvenile plaice was estimated as the ratio between observed field and DEB-predicted maximum growth, i.e. realized growth (RG), for each sampling station. Generalized additive modelling (GAM) (Hastie & Tibshirani, 1990; Zuur et al., 2007) was then used to describe the temporal variation in RG in each habitat (as not enough data was available for an analysis with individual sampling stations) and to compare patterns between years (1986 and 2009). GAM's were fitted to the RG data using the mgcv package (Wood, 2006) in R environment (R Development Core Team, 2014). Models were applied to each habitat in each year using the formula:

$$RG_i = \alpha + f(daynr_i) + \varepsilon_i$$

Where RG_i is the realized growth for observation i, which is modelled as a smoothing function of day of the year, α is the intercept and ε_i the residual (unexplained information or noise). Cross-validation was used to estimate the optimal amount of smoothing for each smoother (Wood, 2006).

For the interannual comparison of RG-time patterns a model with *year* (nominal) as explanatory variable was used. Two nested models were compared:

$$RG_i = \alpha + f(daynr_i) + factor(year_i) + \varepsilon_i \qquad \text{(M1)}$$

$$RG_i = \alpha + f_1(daynr_i) + f_2(daynr_i) \times factor(year_{2009,i}) + factor(year_i) + \varepsilon_i \qquad \text{(M2)}$$

In (M1) we assume that both years have the same RG-time relationship and hence, only one smoothing curve is used. The second model (M2) allows for a change in the RG-time relationship between years and thus includes two smoothers: the first *daynr* smoother represents the overall time effect on RG in the two years while the second represents the deviation in year 2009 from the overall RG-time relationship. Model comparison was done with a likelihood ratio test as both models were nested (Wood, 2006). The inter-habitat variation in RG temporal patterns within the year was examined using the same approach but with *habitat* (nominal) as explanatory variable. The two nested-models compared were as follows:

$$RG_i = \alpha + f(daynr_i) + factor(habitat_i) + \varepsilon_i \qquad \text{(M3)}$$

$$RG_i = \alpha + f_1(daynr_i) + f_2(daynr_i) \times factor(habitat_{subtidal,i}) + factor(habitat_i) + \varepsilon_i \quad \text{(M4)}$$

3. RESULTS

3.1. (A)biotic conditions

Water temperatures measured at the various intertidal stations during high water varied from 6.7 ± 2.6 °C (mean±sd) in mid-March 2009 to a maximum of 20.3±0.8 °C in August. These were higher than temperatures recorded in 1986, especially during spring months (Fig. 2) although the differences were not statistically significant (t-test; t_{14}=-1.224, p>0.05). Temperatures measured during both sampling periods matched the general temperature patterns from the NIOZ jetty time series (Fig. 2). Mean temperatures in spring (March to May) 1986 were 3.4 °C lower than in 2009. Differences in mean water temperatures between the various habitats in 2009 based on modelled data were assessed using one-way ANOVA. The intertidal had the lowest average monthly temperatures (mean±se: 11±0.7°C) and the highest maximum monthly values (15.0±0.8°C) but the differences of about 0.4°C among habitats were not statistically significant (p>0.05).

A wide range in mean total macrozoobenthos biomass values was found in the different habitats in 1986 and 2009, with highest mean values observed in the subtidal in both years (Fig. 3). In 2009, biomass values up to 150 g AFDM m^{-2} were measured. The patterns in total biomass across stations in the 2 years were not correlated with each other (Spearman rank correlation test, p > 0.05, n=18) indicating that the ranking of food-rich and poor stations had changed. The macrozoobenthic invertebrate composition in the areas sampled consisted mostly of bivalves and polychaetes with a few species contributing to total biomass (for 2009 data see Supplementary information Table S1).

Potential food biomass for 0-group plaice was on average an order of magnitude lower than the total benthic biomass values, between 4 – 10 g AFDM m^{-2} (Fig. 3). Highest mean values were found in the intertidal in 1986. Mean values were lower in 2009 in all habitat types compared to 1986, despite increased total biomass values in the subtidal and the tidal channels in 2009. Potential food biomass and total benthic biomass were highly positively correlated in 1986 (Spearman rank correlation test, r_s=0.59, p<0.001) but not in 2009 (r_s=is 0.30, p>0.05). There was a positive trend between potential food biomass across stations in the 2 years, however the relationship was not significant (r_s=0.45; p>0.05, n=18).

3.2. 0-group plaice

In 1986, newly-settled plaice (≤15 mm) were first found in the intertidal from April onwards, while in 2009, early post-settled plaice were already present by the time of the first survey, in mid-March, indicating an earlier settlement. In both years, densities in the intertidal peaked in May decreasing rapidly thereafter (Fig. 4a,d). The seasonal patterns of 0-group plaice abundance in subtidal and tidal channels differed between years. In 1986 numbers in the subtidal declined after settlement but increased again in autumn (Fig. 4b) and in channel stations, low densities were observed throughout the sampling period with maximum numbers found in autumn (Fig. 4c). In contrast, in 2009 0-group abundance increased up to peak values at around June, followed by a steep decrease and low numbers until the end of the year (Fig. 4e,f). Overall, the intertidal presented higher numbers of 0-group plaice in 1986 with peak densities in the range of 50 to 870 ind.$[10^3 \text{ m}^2]^{-1}$ depending on the station, while subtidal ($10 - 295$ ind. $[10^3 \text{ m}^2]^{-1}$) and channels ($6 - 220$ ind. $[10^3 \text{ m}^2]^{-1}$) had much lower values. In 2009, on the contrary, 0-group plaice was clearly more abundant in deeper habitats: peak densities at the intertidal were between $60 - 170$ ind. $(10^3 \text{ m}^2)^{-1}$, compared to $130 - 1150$ ind. $(10^3 \text{ m}^2)^{-1}$ in the subtidal and $170 - 750$ ind. $(10^3 \text{ m}^2)^{-1}$ in tidal channel stations.

The depth distribution of the 0-group plaice showed distinct patterns between years (Fig. 5). In 1986, the median depth remained between 1.5 and 2 m throughout most of the study period, increasing only after October. In 2009, 0-group plaice were found at very shallow areas in mid-March, at the time of the first survey (median depth: 0.8 m), and then, up till mid-July the sampled population was found at increasingly deeper areas. Thereafter, median depth declined to 2-3 m until the end of the sampling, possibly due to the offshore emigration of larger individuals.

Mean length of 0-group plaice increased continuously until early October in 1986 in all habitats (Fig. 6). In the intertidal, growth was generally higher but also more variable than in the subtidal (Table 1) with a size range at the end of the growing season of 80 to 100 mm and 60 to 80 mm, respectively (Fig. 6a,b). In 2009, mean length in intertidal stations, increased until mid-July (Fig. 6d) and up to mid-August in the deeper stations (Fig. 6e,f). For comparison of the 0-group plaice size at the various stations, mean values in August were taken which ranged from 73 to 95 mm in the intertidal, 80 to 100 mm in subtidal stations (Fig. 6e), and 87 to 110 mm in the tidal channels (Fig. 6f). Differences in mean sizes among the three habitats in 2009 were tested using nested ANOVA with stations as the nested factor. Although a (barely) not statistically significant ($F_{2,15}=3.63$, $p=0.052$) difference was found, mean length in channels was clearly higher than at the intertidal habitat (Tukey HSD post hoc test: $p<0.05$).

For the relationship between 0-group plaice growth and food biomass at each habitat, comparisons were restricted to specific periods of the growth season to exclude bias caused by larval immigration early in the season and size-dependent emigration in

the later part of the season. Different periods were considered for 1986 (1 June to 1 October) and 2009 (1 May to 15 July) (Table 1) reflecting the differences in seasonal distribution and abundance patterns found in the 2 years. In 1986, a significant positive correlation between growth and food was found for the intertidal (Spearman rank correlation test $r_s = 0.93$; n=6), while no relationships were found in any of the habitats in 2009 (p> 0.05).

3.3. Realized growth

In all habitats in both years, realized growth (RG) decreased over time, indicating an increasing discrepancy between observed field growth and model predictions at unlimited food (Fig. 7). The declines were nonlinear and significant at the 5% significance level. RG values were initially high at the beginning of the season declining thereafter and stabilizing from August onwards. Final models excluded the existence of interactions meaning that temporal variation patterns in RG were similar between habitats and years (Table 2). Significant differences in RG absolute values were found between intertidal and subtidal habitats in the 1986 survey (as indicated by a significant smooth term, p<0.01), whereby 0-group plaice in the intertidal exhibited higher realized growth for a comparable sampling period (mid-May to mid-September). In 2009, all habitat types displayed similar RG-time trends and no significant differences in absolute RG values were found (p= 0.334). In 2009, comparisons were restricted up till end of July to avoid bias caused by plaice movements towards deeper waters.

4. DISCUSSION

4.1. Habitat use

This study shows distinct patterns of habitat use patterns by age-0 plaice in the mid-1980s compared to nowadays for the western Dutch Wadden Sea region. For juvenile plaice, the ecological function of each habitat type, in this region has been previously established showing that intertidal flats were the primary nursery habitat during plaice first year of life (Zijlstra et al., 1982; Van der Veer & Witte 1993). Despite performing tidally movements onto and off the intertidal to deeper areas associated to feeding (Kuipers, 1973; van der Veer & Bergman, 1986), migrations were considered of minor importance up till August and no severe decline in abundances were seen before September (Zijlstra et al., 1982; van der Veer, 1986; van der Veer & Witte, 1993). In agreement with recent observations for the Balgzand, a well-studied tidal flat area in western part of the Wadden Sea (van der Veer et al., 2011), this study shows that 0-group

plaice also disappears from several other intertidal areas already in early summer and the high abundances found in subtidal and tidal channels suggest that deeper habitats nowadays can contain and support large populations of young-of-the-year plaice. The fact that these patterns were also observed in 2010, when half of the sampling stations were revisited (van der Veer & Witte, unpubl. data) indicates that a shift in habitat use is not a single year event. Residence in intertidal areas is also shorter than before and, by mid-July most 0-group plaice has disappeared from the intertidal at high water. The succession in seasonal abundance patterns between depth strata suggests that a substantial part of the subtidal populations originate from movements of the intertidal one, which presently take place much earlier than before.

The shifting importance of subtidal areas as main nurseries for 0-group plaice requires an evaluation of whether successful settlement of larval plaice is still restricted to the intertidal zone. In both years, newly-settled plaice were only found in intertidal stations. Although different gears were used to sample intertidal and subtidal and channel areas, this pattern is not likely to be a sampling artifact since the catch efficiency of the larger 3 m beam trawl for just-settled plaice is in the order of 35 % (Bergman et al., 1989) which is substantial enough to retain small sized plaice. Additional years of high-frequency sampling at these sites during the settlement period, preferably using similar gears, are required to evaluate the stability of these patterns in habitat selection.

A proposed mechanistic explanation for the observed shifts in juvenile plaice distribution advocates that this is a species response to maximize their physiological performance during the growing season (Teal et al., 2012). Using a bioenergetics modeling approach to predict growth potential of juvenile plaice in the North Sea, Teal et al. (2012) showed that, as a result of the interplay between water temperatures exceeding limits of tolerance of juvenile plaice and food resources available, the habitat quality of coastal areas has declined and that the most suitable summer habitat in terms of growth potential moves offshore and further north as size increases (Teal et al., 2012). In addition, increased habitat quality of offshore areas promoted by a release of competitive pressure and/or predation mortality due to declines in larger predatory fish has also been suggested as potential causes for distribution shifts (van Keeken et al., 2007).

Whilst these mechanisms may explain the observed retreat of older juvenile (I- and II- group) plaice from the western Wadden Sea in recent years, whether it also holds for the 0-group shift in inshore waters from the intertidal to deeper areas in early summer is not clear. Thermal and food effects on growth potential are strongly size-dependent and as Teal et al. (2012) showed, larger size classes (> 20 cm) are more prone to suffer from food limitation (due to increased metabolic demands at higher temperatures) rather than smaller sized (0-group) individuals with higher optimum and upper tolerance limits (van der Veer et al., 2009). In this respect, water temperatures measured in the various

intertidal stations were well within the physiological tolerance range described for 0-group plaice (Freitas et al., 2010) and, in addition, no clear differences in thermal regimes between the different habitats were found. We cannot exclude, however, that actual thermal environment experienced by 0-group plaice is insufficiently captured by the modelled temperature data, despite validation of the model against several observational datasets (Duran-Matute et al., 2014). Not only may the dynamic nature of shallow tidal areas such as the Dutch Wadden Sea lead to less precise estimates but also fine-scale habitat selection by individuals (van der Veer & Bergman, 1986; Hurst et al., 2010) and/or fine-scale spatial thermal heterogeneity (Budy et al., 2011) may occur hampering the possibility of linking species response to thermal conditions.

Flatfish distribution and habitat choice are also influenced by food availability (McIntyre & Eleftheriou, 1968; Pihl & van der Veer, 1992). In fact, food resources are amongst the most important determinants of habitat quality for young flatfish (Gibson, 1994; 1997). However, field assessments of these relationships are seldom done due to the difficulty in quantifying the abundance of appropriate prey items (Stoner et al., 2001; but see van der Veer & Witte, 1993). Benthic macroinvertebrates are an important food source (Gibson, 1994; de Vlas 1979; Amara et al., 2001) and juvenile flatfish can feed not only on whole prey items but also on regenerating body parts such as bivalve siphon tips and polychaete tails tips, heads and tentacles (Kuipers, 1977; Ansell et al., 1999; van der Veer et al., 2011). Using qualitative information from 0-group plaice diet, combined with macrozoobenthic biomass data from specific surveys in intertidal and subtidal areas of the western Dutch Wadden Sea we conclude that, although subtidal areas present much higher total macrobenthic biomass, the amount that is actually available for 0-group plaice does not differ significantly between areas, which suggests that food *per se* may not explain the redistribution patterns of 0-group plaice in early summer. However, as with environmental temperature patterns, small-scale spatial variation in feeding conditions may occur which limits the characterization of prey environment available for plaice. The intertidal benthic assemblage composition of the Wadden Sea is strongly associated with the abiotic environment resulting in a biologically and environmentally heterogeneous system (Compton et al., 2013) with a patchy distribution of resources. In addition, juvenile plaice can exhibit trophic flexibility at very small spatial scales (Mariani et al., 2011; de Raedemaecker et al., 2011) suggestive of complex and variable feeding strategies.

4.2. Habitat quality

Growth is typically considered as a reliable indicator of the relative quality of distinct areas occupied by juvenile fish (Gilliers et al., 2006; Searcy et al., 2007; Glass et al., 2008; de Raedemaecker et al., 2012). The shift in main nursery habitat does not appear

to be caused by reduced growth rates in the intertidal as the observed growth in this study was similar to reported in mid-80s (van der Veer & Witte, 1993). For subtidal areas, however, it seems that growth has improved but, while in the 1980s, growth rates were positively correlated (although not statistically significant) with prey conditions (both quantity and quality) no such relationships were found in 2009. Subtidal areas now have a lower potential food biomass (considering suitable prey items for plaice) and there is no evidence for an improvement in abundance of key prey species like the lugworm *Arenicola marina*. Factors other than feeding conditions may therefore have contributed to the observed improved growth in the subtidal.

Growth conditions are also temporally dynamic. Growth estimates based on shifts in size-frequency distributions can potentially be biased by size-selective mortality and migration processes. The fact that a similar pattern of progressive decrease in realised growth throughout summer was observed in all the habitats analyzed in both periods, even in channels where densities did not decrease but rather increased, suggests that size-selective migration movements cannot explain the observed patterns. Furthermore, there is no strong support for size-selective predation by fishes and birds on 0-group plaice in summer (van der Veer et al., 1997). The results of this study are also in line with previous observations for the Balgzand intertidal (Teal et al., 2008; van der Veer et al., 2010), as well as for a number of European nurseries (Ciotti et al., 2010; Freitas et al., 2012; Ciotti et al., 2013a,b). This again suggests that variations in food conditions and hence growth potential cannot explain the shifts in habitat use between 1986 and 2009. Several mechanisms for the observed growth reduction in 0-group plaice in summer have been suggested (see review in Ciotti et al., 2014), including competition and reduced prey activity (van der Veer et al., this issue), however, at present, the precise underlying mechanism(s) remains elusive.

4.3. Nursery capacity of the Wadden Sea

The international Wadden Sea and the bordering coastal zone is the most important nursery area for North Sea plaice (Zijlstra, 1972; Rijnsdorp & van Beek, 1991). Conditions provided by and experienced within the nursery are considered to be important for plaice recruitment with a potential bottleneck effect on populations' life cycle (van der Veer, 1986; Bergman et al., 1988; van der Veer et al., 2015). However, nursery conditions vary or can even show shifts over time. In the last 25 years, mean annual water temperature has increased significantly in the western Wadden Sea by 1.5°C (van Aken, 2008). This increase has been suggested to have an impact on juvenile plaice by putting this cold water species at the verge of its temperature tolerance range (Freitas et al., 2010). Since this increase might be most pronounced in summer in shallow waters, this might explain

the disappearance of juvenile plaice including 0-group from the intertidal (c.f. Teal et al., 2012). Also macrozoobenthos biomass fluctuates over time. Previous observations (van der Veer et al., 2011) and also this study illustrate that total macrozoobenthic biomass is not a good indicator of plaice feeding conditions. On average only about 10% of the total macrozobenthic biomass appears to be available as potential prey items for 0-group plaice (van der Veer et al., 2011). Compared with 1986, potential food densities in 2009 were lower in all three habitat types, especially in the intertidal, despite higher total biomass values in both the subtidal and tidal channels. To what extent this reflects a general trend in overall food availability is unknown at present. It is also unclear whether food availability for 0-group plaice is the key factor for growth since growth patterns were similar in both periods in all habitat types.

Despite the various clear shifts in habitat use by juvenile plaice, the Wadden Sea is still able to support the young-of-the-year plaice population. Interestingly, in spite of the disappearance of older juveniles from the area, there is no evidence for an effect at the adult population level. In fact, North Sea plaice stock has even been increasing in the last years, being at its highest level since its first assessments in 1957 (ICES, 2014). If on the one hand this could suggest that the export capacity of the area has remained the same, on the other hand one cannot exclude that additional production is coming from other nursery habitats around the North Sea. Since densities did not increase in the coastal zone (Tulp et al., 2008), it seems that within the Wadden Sea, despite the relative importance of the various habitats (intertidal, subtidal, tidal channels) has changed, the function of the intertidal area has been compensated for. The same has been observed in western Swedish coastal waters, where despite habitat deterioration, enhanced plaice recruitment has been observed in recent years (Cardinale et al., 2010). This highlights the fact that the presence and quality of alternative habitats is at least as important to consider when evaluating the nursery capacity for fish populations and that nursery grounds are dynamic entities expanding, contracting and shifting in location over time (Stoner et al., 2001). Future research should focus on determining the relative importance of distinct areas by assessing their contribution to the adult stock as well as fish movement and habitat use. In this respect, natural tags like elemental otolith fingerprinting (Fodrie and Levin, 2008; Vasconcelos et al., 2008) and tissue stable isotopic signature (Herzka, 2005; Reis-Santos et al., 2015) can be valuable tools.

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List of Tables and Figures

Table 1. Growth (mm) based on the increase in mean length of 0-group plaice estimated by linear regression, at the various sampling stations in 1986 and 2009.

Station code	Growth (±SE) (mm)	
	1986	2009
	1 Jun – 1 Oct	1 May – 15 July
Intertidal		
1	51 (5.9)	28.9 (0.8)
2	44 (5.5)	56.9 (4.0)
3	45 (7.8)	59.3(12.3)
4	63 (9.4)	42.2 (6.7)
5	51 (6.6)	48.2 (5.6)
6	52 (9.4)	63.6 (4.3)
Subtidal		
11	44 (1.8)	28.6 (1.1)
12	39 (6.2)	43.2 (4.2)
13	32 (6.4)	39.6 (3.9)
14		36.7 (12.5)
15	31 (5.8)	40.9 (0.6)
16	30 (8.0)	44.9 (0.3)
Tidal channel		
21		37.5 (6.1)
22		45.7 (8.0)
23		40.6 (−)
24		44.1 (0.6)
25		55.2 (2.1)
26		51.5 (1.3)

Table 2. Outcomes of final generalized additive models (GAM) (without interactions) for interannual (1986, 2009) and inter habitat (intertidal, subtidal, channel) variations in realized growth (RG) of 0-group plaice.

|	Estimate	Std. err.	t-value	p-value		EDF	F	R^2	p-value
Interannual comparison (1986, 2009)									
Intertidal									
Intercept	0.71	0.08	9.01	< 0.001	s(Daynr)	1	17.75	0.38	<0.001
Factor(Year2009)	-0.13	0.10	-1.24	0.23					
Subtidal									
Intercept	0.29	0.05	6.28	< 0.001	s(Daynr)	1	17.79	0.40	<0.001
Factor(Year2009)	0.04	0.06	0.66	0.52					
Inter habitat comparison									
1986									
Intercept	0.56	0.05	10.38	<0.001	s(Daynr)	1	19.06	0.53	<0.001
Factor(HabitatSubtidal)	-0.25	0.08	-3.14	<0.01					
2009									
Intercept	0.69	0.06	12.46	<0.001	s(Daynr)	1.51	39.34	0.54	<0.001
Factor(HabitatIntertidal)	-0.12	0.08	-1.50	0.14					
Factor(HabitatSubtidal)	-0.06	0.08	-0.79	0.43					
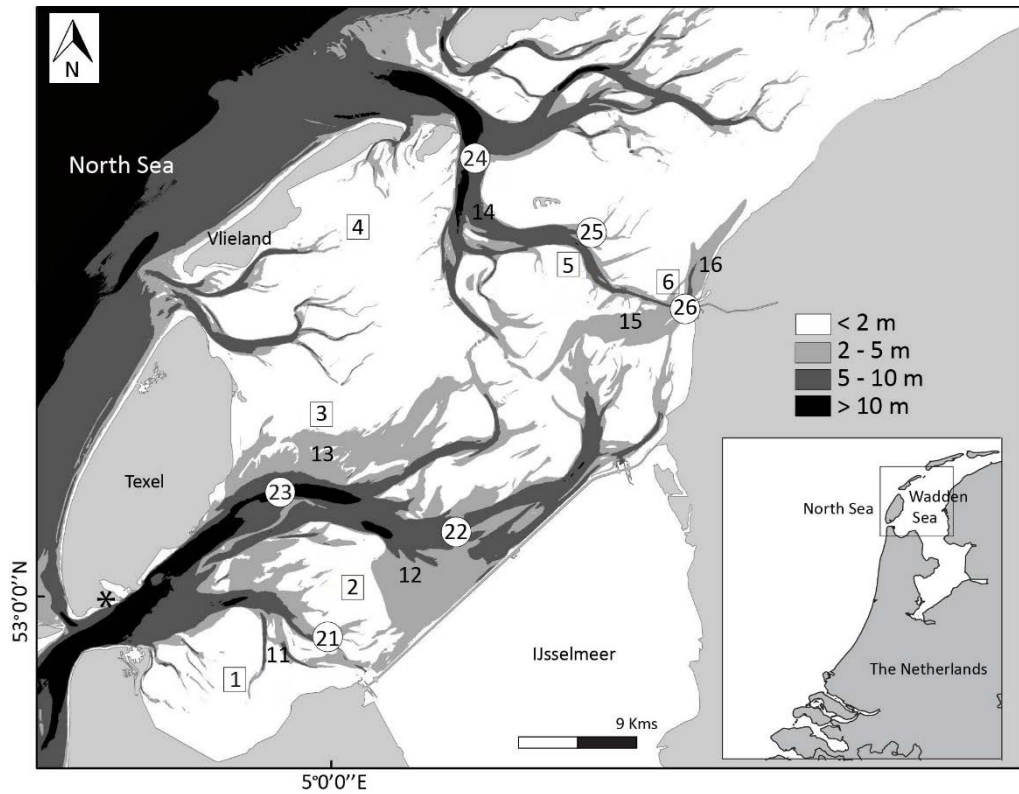
Figure 1   Location of sampling stations in the western Dutch Wadden Sea. Stations 1 to 6: intertidal stations; Stations 11 to 16: subtidal stations; Stations 21 to 26: tidal channels. Station numbers refer to code used in Van der Veer & Witte (1993). Different shades refer to different depth strata. The location of the NIOZ jetty, a fixed temperature measurement station, is also indicated (∗).
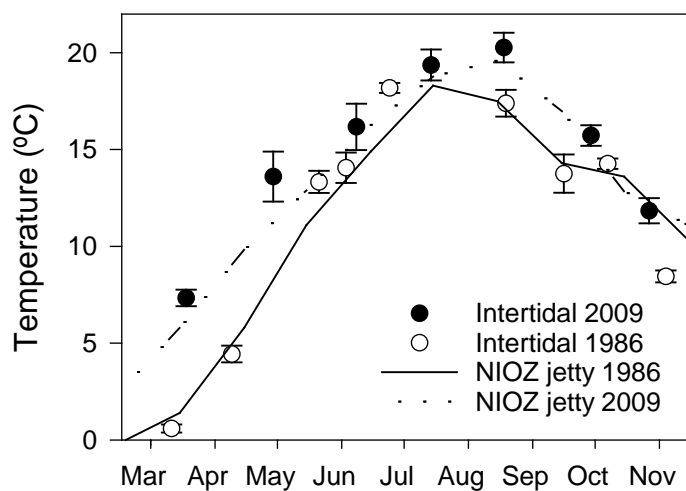
Figure 2 Temperature data for the western Dutch Wadden Sea in 1986 and 2009. Symbols refer to the mean water temperatures (±SD) measured at high water in the various intertidal stations at the time of fish sampling. Lines are the average temperatures derived from continuous measurements at the NIOZ jetty in the Marsdiep tidal inlet (van Aken 2008).
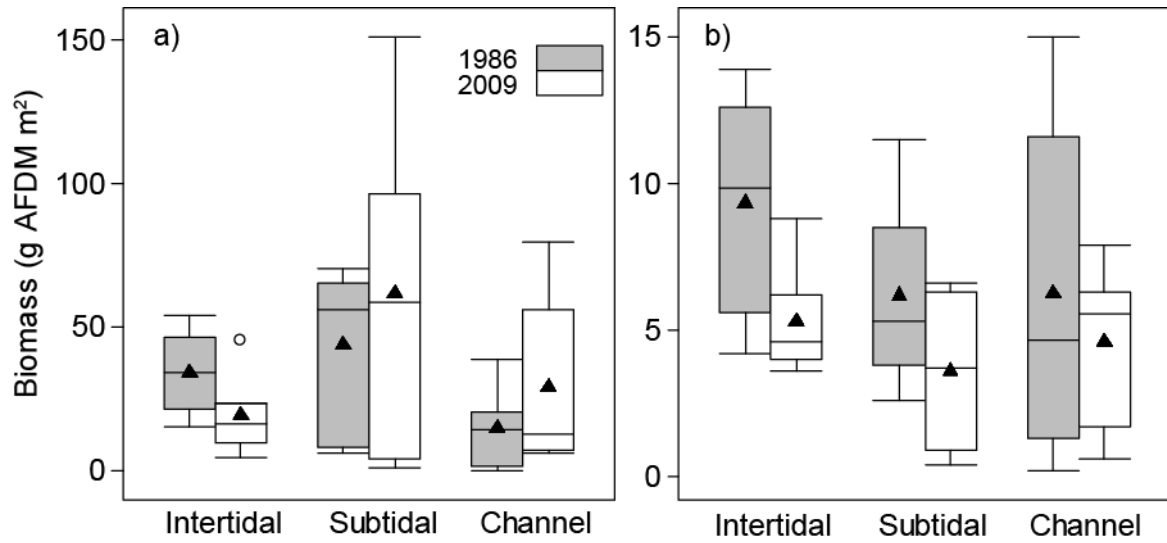
Figure 3 a: Total macrozoobenthic biomass (g AFDM m^{-2}) and b: potential food for 0-group plaice at the various habitats sampled in the western Wadden Sea in 1986 and 2009. Thick horizontal bars represent medians, boxes indicate the upper and lower quartiles, whiskers represent the range, dots are outliers and triangles indicate mean values.
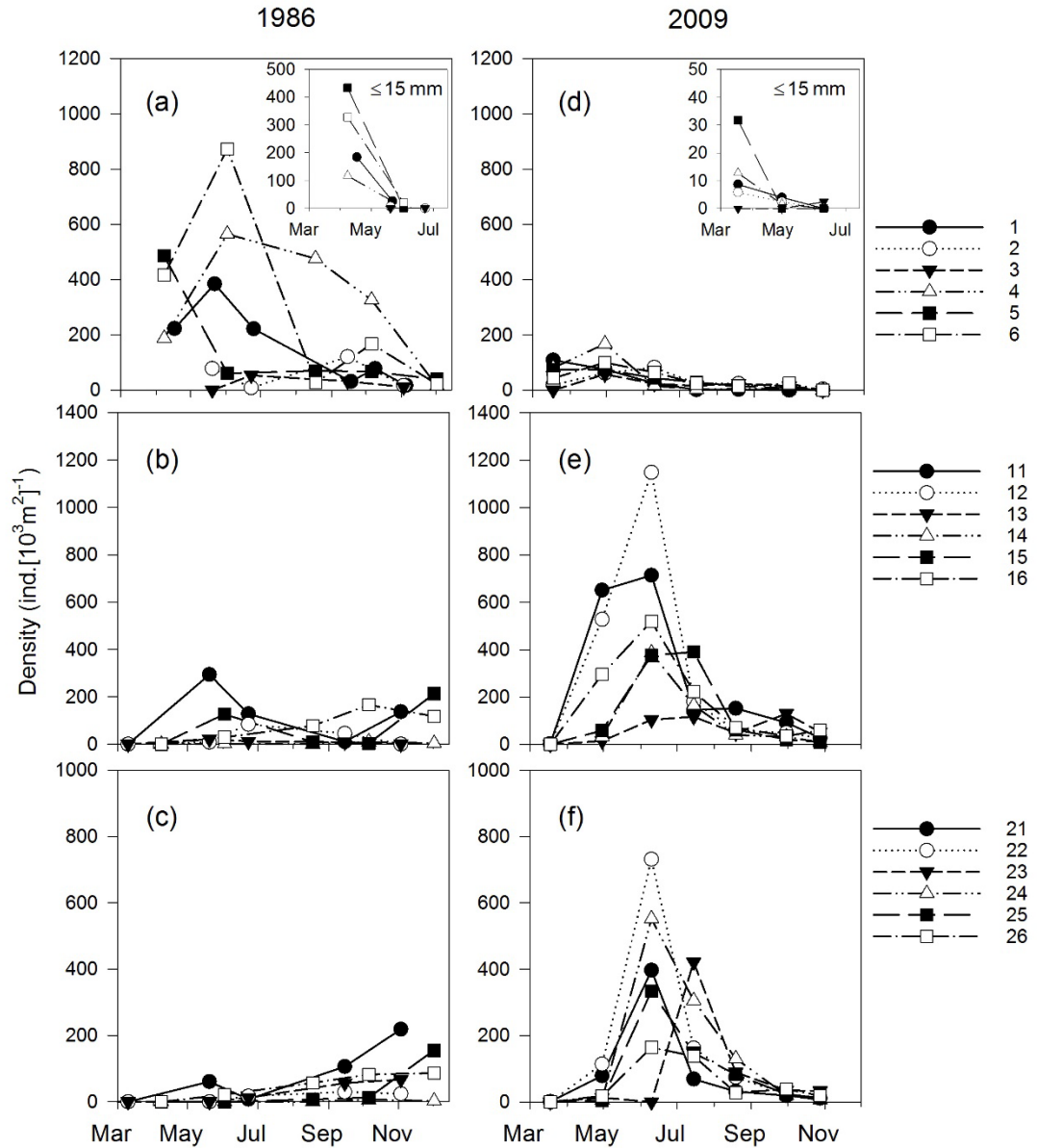
Figure 4   Abundance of 0-group plaice (ind.[10³m²]⁻¹) in 1986 and 2009 at the various a,d) intertidal; b,e) subtidal; and c,f) channel stations of the western Dutch Wadden Sea. Abundance of newly settled plaice (≤15 mm) is also indicated for the intertidal area (see insets in (a) and (b); not present in the other habitats). Y-axis scales are different among habitats. Station numbers refer to locations on Figure 1.
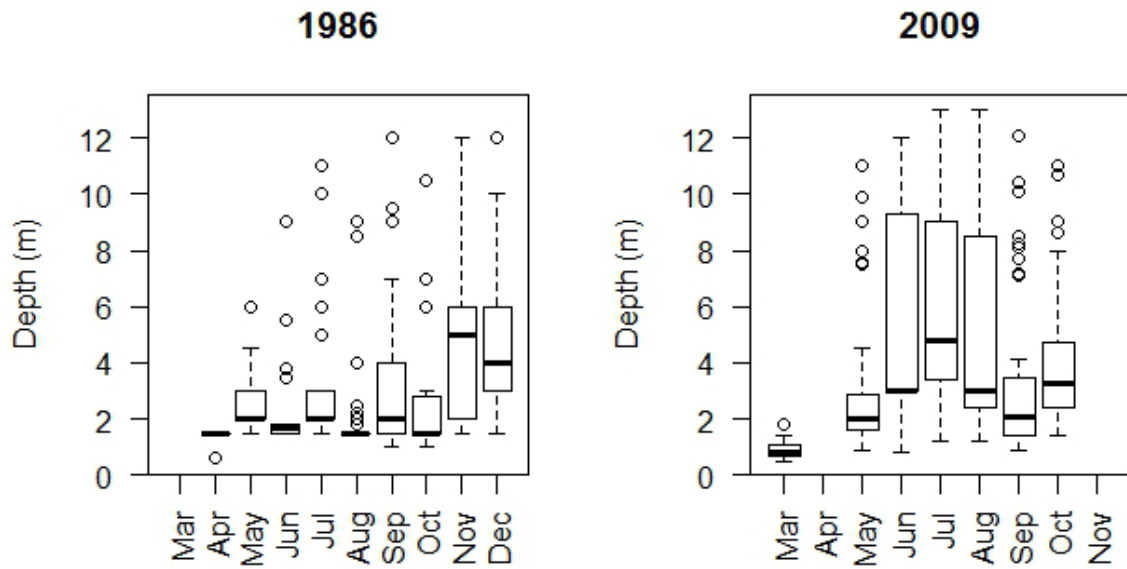
Figure 5. Seasonal variation in 0-group plaice depth distribution (m) in the western Dutch Wadden Sea in 1986 and 2009. Thick horizontal bars represent medians, boxes indicate the upper and lower quartiles, whiskers represent the range and dots are outliers.
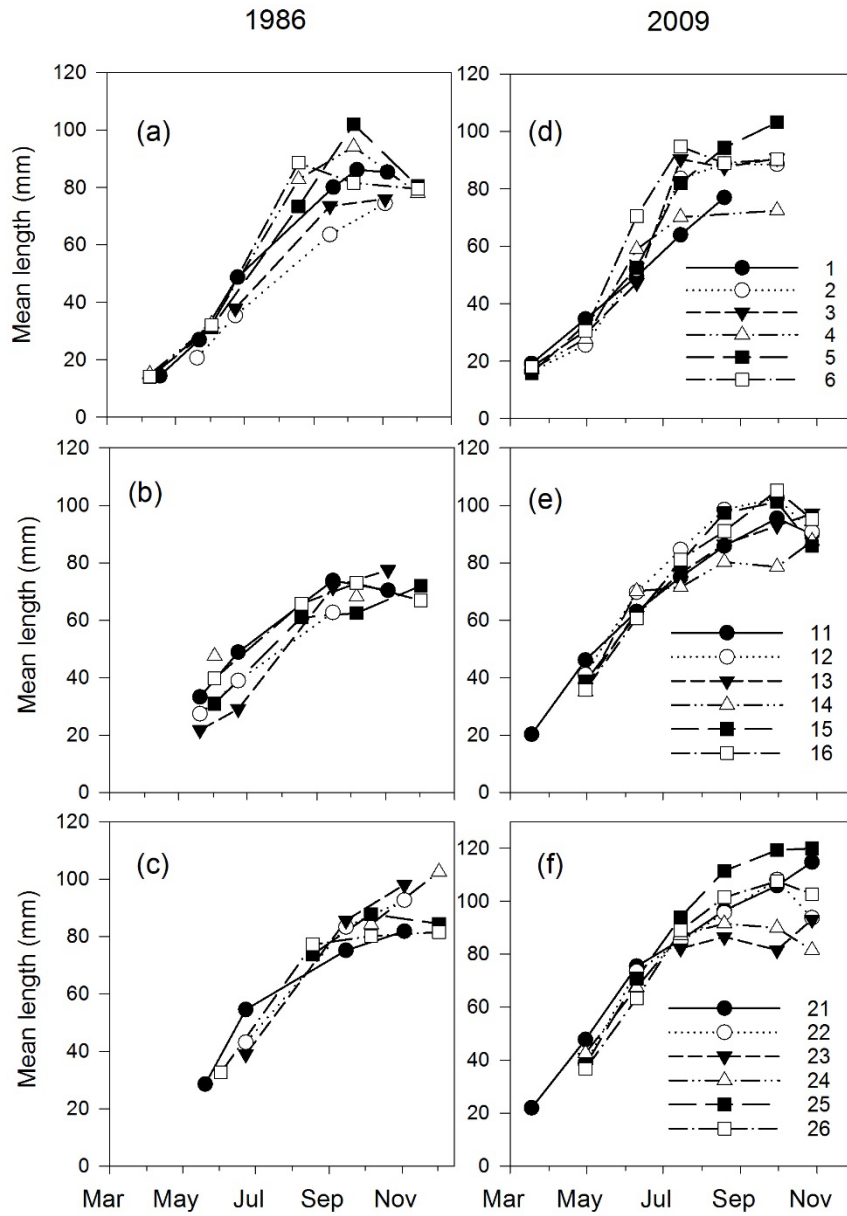
Figure 6 Mean length of 0-group plaice (mm) in 1986 and 2009, at the various a,d) intertidal; b,e) subtidal; and c,f) channel stations of the western Dutch Wadden Sea. Station numbers refer to locations on Figure 1.
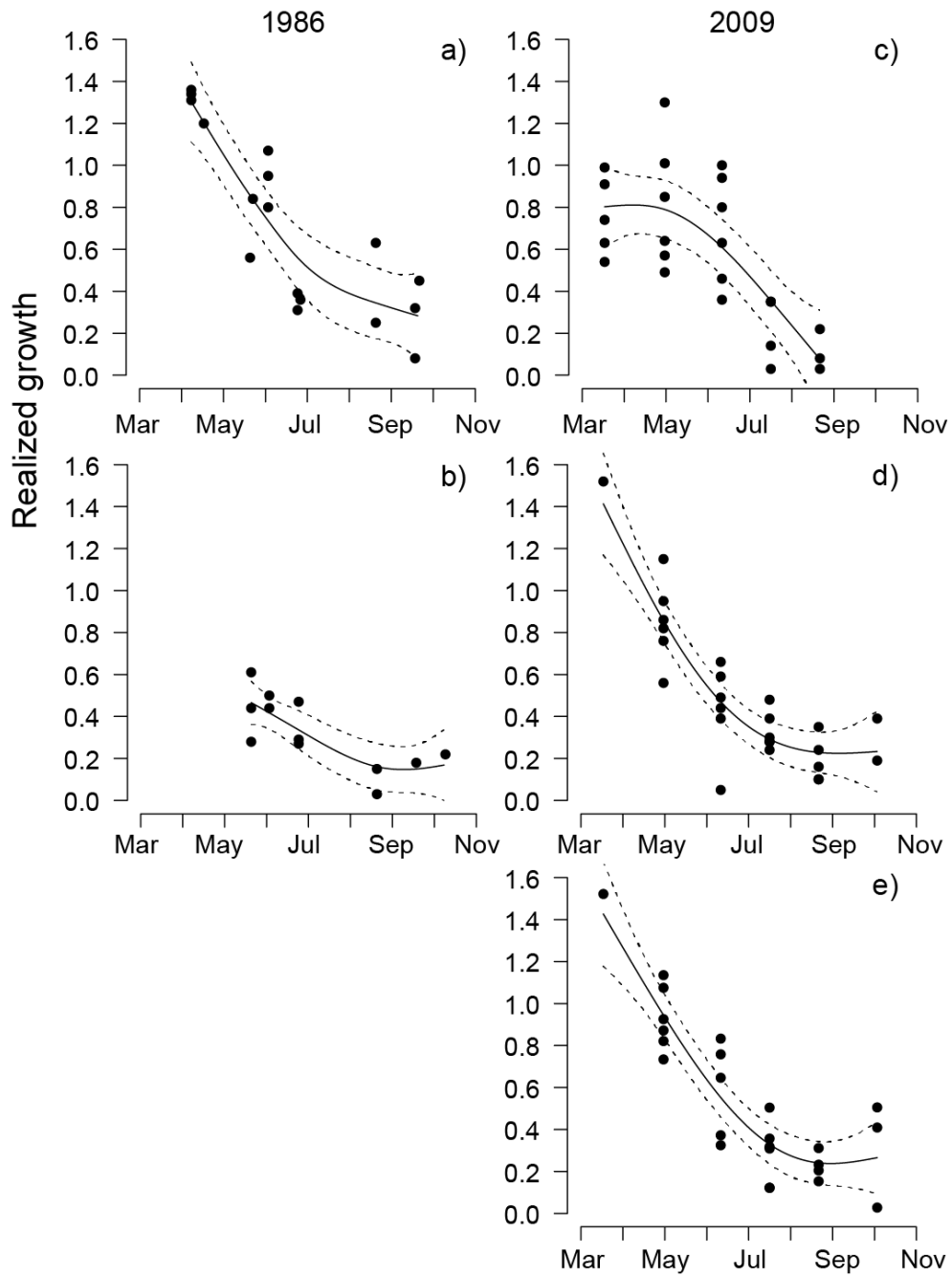
Figure 7 Realized growth (-) ratio between observed field and DEB-predicted maximum possible growth) of 0-group plaice in the western Dutch Wadden Sea in 1986 and 2009 in the various (a,c) intertidal, (b,d) subtidal, and (e) channel stations. Solid lines are the smoother fits of additive modelling of the variation in realized growth over time. Dashed lines indicate 95% confidence bounds.