

Variability in transport of fish eggs and larvae. IV. Interannual variability in larval stage duration of immigrating plaice in the Dutch Wadden Sea

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ABSTRACT: Larval immigration of plaice *Pleuronectes platessa* L. into the western Wadden Sea in spring was followed biweekly from 1993 to 2002. For each year (1993 excluded), 150 settling individuals were selected and used for reconstruction of larval stage duration based on otolith daily ring counts. In addition, prevailing water temperature conditions during drift as revealed from NOAA satellite images were determined. Mean larval stage duration varied between about 40 and 60 d, without any clear significant pattern between or within years. Year-class strength of plaice in the western Wadden Sea was not related to mean larval stage duration. Mean larval stage duration did not show a clear pattern during the period of immigration, nor with reconstructed temperature conditions. The observed decrease of larval stage duration with temperature in the field was lower than that observed under laboratory conditions, suggesting food limitation with increasing temperature during drift. The fact that both within-year and for all years combined the number of immigrating larvae was inversely related to temperature conditions during drift suggested that year-class strength could be affected by temperature-mediated predation, but simultaneously occurring food limitation at high temperatures cannot be excluded.

KEY WORDS: Plaice · *Pleuronectes platessa* · Year-class strength · Larval drift · Larval stage duration · North Sea · Predation · Temperature

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INTRODUCTION

Flatfish species have different life stages characterized by specific habitat requirements, often resulting in spatial separation. Their life cycle typically starts with a pelagic egg and larval stage drifting with the currents. At the end of the larval stage they metamorphose from a symmetrical pelagic larva to a typical flatfish and settle in shallow juvenile nursery areas followed by an adult stage in more open seas (Rijnsdorp et al. 1995). With these spatially separated stages, life cycle closure and connectivity between the various life stages is crucial for successful recruitment.

Differences in population size, both among species and between subpopulations, have been related to the extent of life cycle closure (Gibson 1994, van der Veer et al. 2000a). The size of nursery ground areas, in par-

ticular, has been suggested to be a crucial factor determining recruitment (nursery size hypothesis; Rijnsdorp et al. 1992, van der Veer et al. 2000a), explaining differences between species. This hypothesis may explain the contrast between, for example, the low population size of turbot with its juvenile stage restricted to the surf zone, and the high abundance of dab with its juveniles spread out in the coastal zone in up to 50 m water depth (Bolle et al. 1994, Gibson 1994).

The majority of the annual recruitment of North Sea plaice *Pleuronectes platessa* L. originates from juveniles from the Wadden Sea and its adjacent coastal zone, an estuarine system bordering Dutch, German and Danish coastal waters (Zijlstra 1972, van Beek et al. 1989). These shallow coastal areas are referred to as juvenile nursery areas because of the favourable conditions for growth and survival (Zijlstra 1972, Bergman

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et al. 1988). Year-class strength appears to be determined in North Sea plaice in the open sea before the pelagic larvae arrive and settle in the coastal nursery areas (Brander & Houghton 1982, van der Veer 1986) or in Irish Sea plaice shortly after settlement (Nash & Geffen 2000). Mortality factors later on during the juvenile stage in the nursery areas do not seem to affect the patterns established during the early juvenile stage (van der Veer et al. 1997, 2000a, Leopold et al. 1998).

Previous studies in the early 1980s suggested that year-class strength of plaice in the western part of the Wadden Sea was inversely related to the February seawater temperature at the spawning grounds in the Southern Bight of the North Sea (van der Veer 1986). In the 1990s this relationship was validated (van der Veer & Witte 1999), but its underlying mechanism is still under debate. Previous studies have indicated that interannual variability in hydrodynamic conditions is important (Nielsen et al. 1998, van der Veer et al. 1998, Bolle et al. 2009). Specifically, cold winters in the Southern Bight of the North Sea are associated with persistent winds from the east and these easterly winds induce an atypical water circulation pattern that affects the strength and direction of the tidal and hence residual currents. These conditions are likely to affect larval drift and distributions, and thus successful settlement.

Biotic factors, especially predation in combination with starvation, are also thought to be key to larval year-class strength. In North Sea plaice, an inverse relationship has been found between the number of settling larvae in the western Wadden Sea and the median water temperature during the pelagic period, both within and between years (van der Veer & Witte 1999), whereas for Irish Sea plaice no birth-date selection in early life stages has been observed (Fox et al. 2007). The synchrony in plaice recruitment around the United Kingdom and its negative relationship with seawater temperature is consistent with the hypothesis that temperature affects predation processes during the larval planktonic stage (Fox et al. 2000). Three-dimensional modeling of egg and larval transport in the Irish Sea (Fox et al. 2006, 2009) and the southern North Sea (Bolle et al. 2009, this volume) has revealed the importance of hydrodynamic variability and larval behaviour. However, the contribution of biological interactions such as starvation or predation processes during egg and larval drift remain unquantified.

Larval growth and survival rates often decline during the transition from yolk to exogenous food sources (e.g. Blaxter & Hunter 1982). After feeding is fully established, larvae are more resistant to starvation, as reflected in the increase in number of days to irreversible starvation with larval age in plaice from 6 to

22 d at 7.5 to 11.5°C (Blaxter & Ehrlich 1974). Larval growth is a function of both temperature and food conditions, and the risk of starvation can be more prevalent with increasing water temperature due to the increasing maintenance costs. Therefore the temperature conditions during the pelagic period affect both predation and growth. Extensive field studies carried out between 1947 and 1971 in the Southern Bight to follow plaice egg and larval patches during the pelagic period of development and drift (Harding et al. 1978, Talbot 1978) have identified significant variability in dispersal and in mortality rates. Despite these years of field observations, it has not been possible to disentangle the relative contributions of starvation versus predation, except for the observation that mortality rates are lower during cold winters (Harding et al. 1978).

The present study presents an indirect analysis of the relative importance of pelagic stage starvation versus predation for successful recruitment of plaice to the nursery grounds. Patterns in abundance of settling larvae that successfully recruited to a nursery ground in the western Dutch Wadden Sea were followed for a 10 yr period (1993–2002) and related to reconstructed variability in larval stage duration from hatching to metamorphosis (1993 excluded—data stored on 4% formalin and therefore unusable) and to temperature conditions during the pelagic period (c.f. van der Veer & Witte 1999). Next, the observed relationship between larval development times and prevailing water temperatures was compared to experimental (Talbot 1977) and other growth data (compiled in Bolle et al. 2009) and deviations were considered to indicate the occurrence of poor growth or starvation conditions. Finally, the relationship between abundance of immigrating larvae and temperature during the pelagic period (c.f. van der Veer & Witte 1999) was tested as an indicator of the importance of predation processes.

MATERIALS AND METHODS

Environmental data. Water temperature of the mixed water column during the pelagic period was obtained from unpublished composites of images from the advanced very high resolution radiometer sensor (AVHRR), installed on board the TIROS-N satellites. Each day, 2 to 4 images of the infrared emitted from the North Sea surface were produced with a spatial resolution of 1.1 km² directly below the satellite. Raw data were corrected for transmission through the ozone layer, Rayleigh scattering and aerosol scattering on the basis of algorithms developed for the Coastal Zone Color Scanner (Roozkrans & Prangmsma 1988). From the Royal Netherlands Meteorological Institute (KNMI) database, daytime images were omitted and only night-

time images were used, to prevent the bias induced from solar irradiative heating of the sea surface. Mean seawater temperature ($\pm 0.6^\circ\text{C}$) was determined from weekly composites from January to June 1993–2002 for 4 stations along a transect between the spawning area and the Marsdiep inlet (Fig. 1a) in the area of plaice egg and larval drift (Talbot 1978). Monthly composites of night images were also compiled for the same time period. Data for the years 1993 to 1997 are published in van der Veer & Witte (1999).

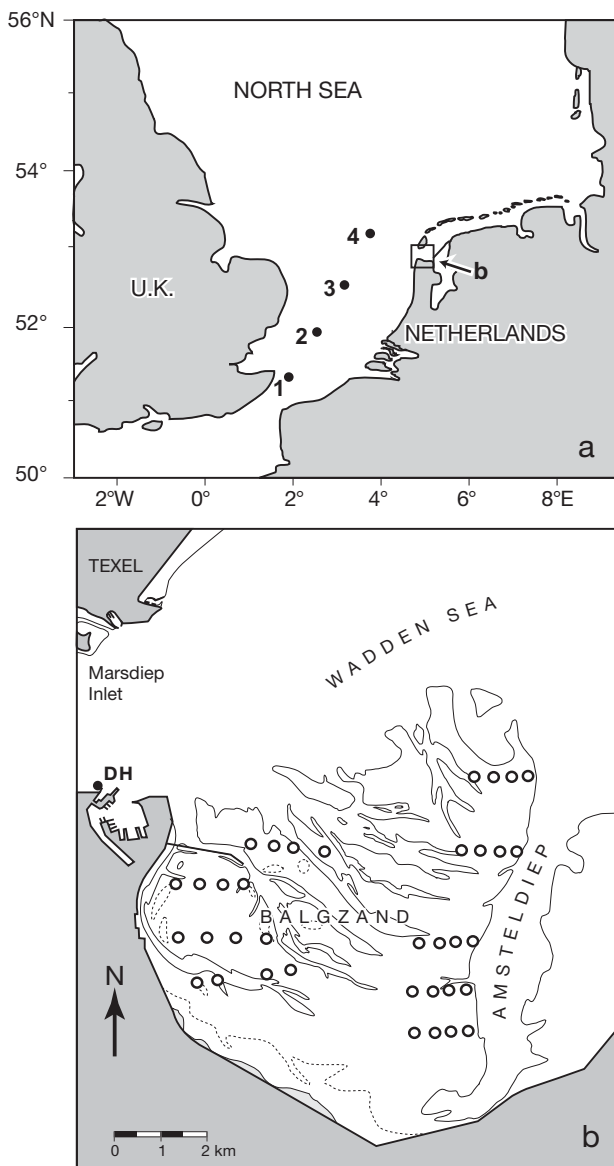


Fig. 1. (a) NOAA satellite water temperature sampling stations (Stns 1 to 4) in the southern North Sea on the transect from the spawning area towards the Marsdiep inlet. For exact positions see Table 1 in van der Veer & Witte (1999). (b) Flat-fish sampling stations (O) at the Balgzand tidal flat area. DH: Den Helder

Hydrodynamic variability in the Marsdiep inlet was expressed as the variability in water supply to the Balgzand intertidal at high water. Five automatically registering tidal gauges were installed around this large, isolated tidal flat system bordering the Marsdiep tidal inlet (Fig. 1b) during the period of larval immigration in 1980–1982. For each high water, the total volume of water covering the Balgzand intertidal was determined and related to the actual observed high water level of the nearby station Den Helder (Fig. 1b). Subsequently, this relationship was applied to estimate the water volume at each high water for the period of larval immigration during 1993–2002.

Larval data. Information on larval abundance was reconstructed from data on settled plaice ≤ 15 mm, since these two are directly related (van der Veer 1986). During the period 1993–2002, demersal samples were collected at Balgzand. Sampling normally commenced in February and continued at frequent intervals (bi-weekly to monthly) on a grid of 36 stations distributed over the area (c.f. Kuipers 1977). Samples were collected during a period of 3 h around high water, since during this period the plaice population is randomly distributed over the area (Kuipers 1977). Hauls of about 100 m in length were undertaken during daytime with a 1.9 m beam trawl with 1 tickler chain and a net mesh size of 5×5 mm, towed by a rubber dinghy with a 25 HP outboard motor at a speed of approximately 35 m min^{-1} (Riley & Corlett 1966). Location of the hauls was established during the first years by wooden poles and later by GPS; the exact length of the hauls was measured with a meter wheel fitted to the trawl.

Catches were deep-frozen and sorted within a few days. All 0-group plaice (except in 1993) were preserved in 70% ethanol and subsequently measured to the nearest mm total length. Numbers caught were corrected for size-selective mesh and catch efficiency after Kuipers (1975) and Dapper (1978) and were converted into numbers per 1000 m^2 (ind. $[10^3 \text{ m}^2]^{-1}$). The arithmetic mean abundance of 0-group plaice ≤ 15 mm, calculated for all stations sampled during a cruise, was considered to reflect the pattern of immigrating larvae (cf. Kuipers 1977, Zijlstra et al. 1982). Maximum observed densities of all 0-group plaice during sampling was taken as an index of year-class strength (cf. Zijlstra et al. 1982, van der Veer 1986).

A subsample of 150 settled plaice ≤ 15 mm was selected in each year (except 1993) for further analysis. Individuals were selected randomly from all cruises, proportional to the abundance determined from each cruise. Sagittal otoliths were removed from the selected fish and mounted for microstructure analysis of daily increments. Preparation of the otoliths was carried out according to standard techniques as described in

van der Veer et al. (2000b). Series of light micrographs at magnifications between 100× and 2500× were used for increment analysis covering the area from the hatching ring to the metamorphosis ring, representing the pelagic period (Ryland 1966, Fox et al. 2007). At least 4 counts of the number of daily increments were made along various radial lines from the first visible increment. If the difference between one of the counts and the mean exceeded 10%, the otolith was removed from further analysis. Counts were corrected for uncertainty in the identification of early increments by interpolation over the distance between the hatching ring and the first clearly defined increment, using an average otolith growth rate of $0.6 \mu\text{m d}^{-1}$ (Hovenkamp 1991, Fox et al. 2007). From these daily increments in combination with date of sampling, hatch date was back-calculated and was used to reconstruct the temperature conditions experienced during larval drift based on the NOAA satellite water temperature images (Fig. 1a). Since the relationship between temperature and development rate is a negative exponential function (Talbot 1977), the median water temperature experienced was calculated. Finally, for each sampling date the mean larval stage duration and temperature was estimated. These values represented the pelagic stage duration and the temperatures experienced as larvae for discrete groups of newly settled plaice, groups that may be thought of as settlement cohorts.

Data analysis. Spearman rank correlations were calculated to assess the relationship among years between 2 variables, after determining temporal independence using an auto-correlation function (ACF). In all occasions, the ACF indicated that there was no significant temporal correlation.

Linear regression was applied to model the relationship between larval stage duration as a function of timing of settlement and year. Timing of settlement was modelled as a continuous covariate and year as a categorical variable. The most important underlying assumptions are homogeneity of variance, independence, normality and no patterns in residuals. Homogeneity of variance was assessed by plotting residuals versus fitted values; in all models we achieved homogeneity. Residual trends were checked using a generalised additive model (GAM) (Wood 2004, 2006), in which the residuals were modelled as a smoother (thin plate regression spline) of the variable Time. Time was created as a new covariate, defined as the number of days since the first observation in the experiment. On all occasions, the smoother was not significant, indicating that the residuals did not contain any long-term temporal patterns. We also inspected the residuals for short-term patterns within a year. Because observations were irregularly spaced, the ACF could not be used. Therefore, variograms were used (using Time as

a coordinate); see Pinheiro & Bates (2000) or Zuur et al. (2009) for examples. Residuals within years were correlated, and therefore violated the assumption of independence, leading to inflated p-values in the linear regression model. To solve the problem, the following generalised least squares (GLS) model was applied:

$$\text{Duration}_s = \text{Settlement}_s \times \text{Year}_s + \varepsilon_s \quad (1)$$

$$\text{cor}(\varepsilon_s, \varepsilon_t) = h(s, t, \rho)$$

where the indices s and t represent 2 different days. The term ε_s is the residual at Day s . In an ordinary linear regression model, the correlation function $h(s, t, \rho)$ is 1 if $s = t$, and 0 if $s \neq t$ (independence). In Pinheiro & Bates (2000), various options are presented to model the residual correlation structure. For short time series, such as the one used in the present study, one can use the following residual correlation structure:

$$\text{cor}(\varepsilon_s, \varepsilon_t) = \theta \quad \text{if } s \text{ and } t \text{ are from the same year} \quad (2)$$

$$\text{cor}(\varepsilon_s, \varepsilon_t) = 0 \quad \text{if } s \text{ and } t \text{ are from different years}$$

This correlation structure is called the compound symmetry correlation. The problem with any correlation structures is that the covariate Year and θ may 'compete' for the same information. Therefore, we applied the ordinary regression model in Eq. (1) without any temporal correlation and estimated θ from the residuals using the model:

$$\varepsilon_s = \text{intercept} + \tau_s$$

$$\text{cor}(\tau_s, \tau_t) = \theta \quad \text{if } s \text{ and } t \text{ from the same year} \quad (3)$$

$$\text{cor}(\tau_s, \tau_t) = 0 \quad \text{if } s \text{ and } t \text{ from different years}$$

Hence residuals from the same year are allowed to be correlated with a value of θ .

The estimated θ is then used (as a fixed parameter) in the GLS model (Eq. 1). As a result, we allow for short-term residual dependencies. In fact, for these data, the model with and without temporal correlation gives the same fit and Akaike's information criterion (AIC). By using the compound symmetry correlation in our models, we divert some of the variation from the fixed part of the model (the covariates) to the random part (the residuals) to ensure that we are not violating the independence assumption.

The significance of the interaction term in Eq. (1) was determined using a likelihood ratio test (Pinheiro & Bates 2000, West et al. 2006, Zuur et al. 2009). Similar models are applied on the relationship between pelagic stage duration and the number of settling plaice larvae in relation to reconstructed median temperature during drift.

All calculations were carried out in R version 2.7.0 (R Development Core Team (2008)). The GAM was applied with the gam function in the package mgcv, and the GLS with the gls function in the nlme package.

RESULTS

Environmental data

The weekly mean water temperatures showed a similar pattern at the 4 stations along the transect between the spawning area and the Marsdiep inlet, with decreasing temperatures until the end of February followed by a steady increase until the end of May (Fig. 2). Reliability of the temperature estimates was checked by comparing estimates from NOAA satellite images of Stns 2 and 3 with model predictions from the Delft3D-FLOW hydrodynamic model (Erfteimeijer et al. 2009, this volume) that was used for larval plaice transport studies (Bolle et al. 2009). For 1996 and 2002, reflecting the range of temperatures observed, the estimates based on the NOAA satellite images and the results from the Delft3D-FLOW hydrodynamic model showed a similar pattern and a good correspondence with maximum differences of approximately 1°C (Fig. 3).

Hydrodynamic variability in the Marsdiep inlet expressed in terms of the observed high water level at Den Helder (source: www.waterbase.nl) was on the order of a few meters: from normal Amsterdam water level (NAP) -50 to NAP +200 cm. The total amount of water at Balgzand was directly related to the high water level at Den Helder ($r = 0.98$, $n = 469$); a rise of 1 cm at Den Helder had the effect of supplying an additional $0.5 \times 10^6 \text{ m}^3$ water to Balgzand. This hydrodynamic relationship was used to estimate the variability in water supply at Balgzand at high water over the period of larval settlement 1993–2002 from data on observed high water at Den Helder.

Larval data

Larval immigration lasted 10 to 13 wk on average, from mid-February to the beginning of May. However, in 2002 immigration began in early February and lasted until the second half of April. Although the seasonal patterns were rather similar between years, absolute densities varied (Fig. 4). Settlement started in February–March with peak densities in March–April and lasted normally until the beginning of May. Interannual variability in peak settlement varied by a factor of 7, from 150 to $>1100 \text{ ind. } (10^3 \text{ m}^2)^{-1}$. The surface under the settlement curve was used as an index of larval supply. For those years in which immigration had already started before the first sampling, the start of the larval immigration was set at 15 February.

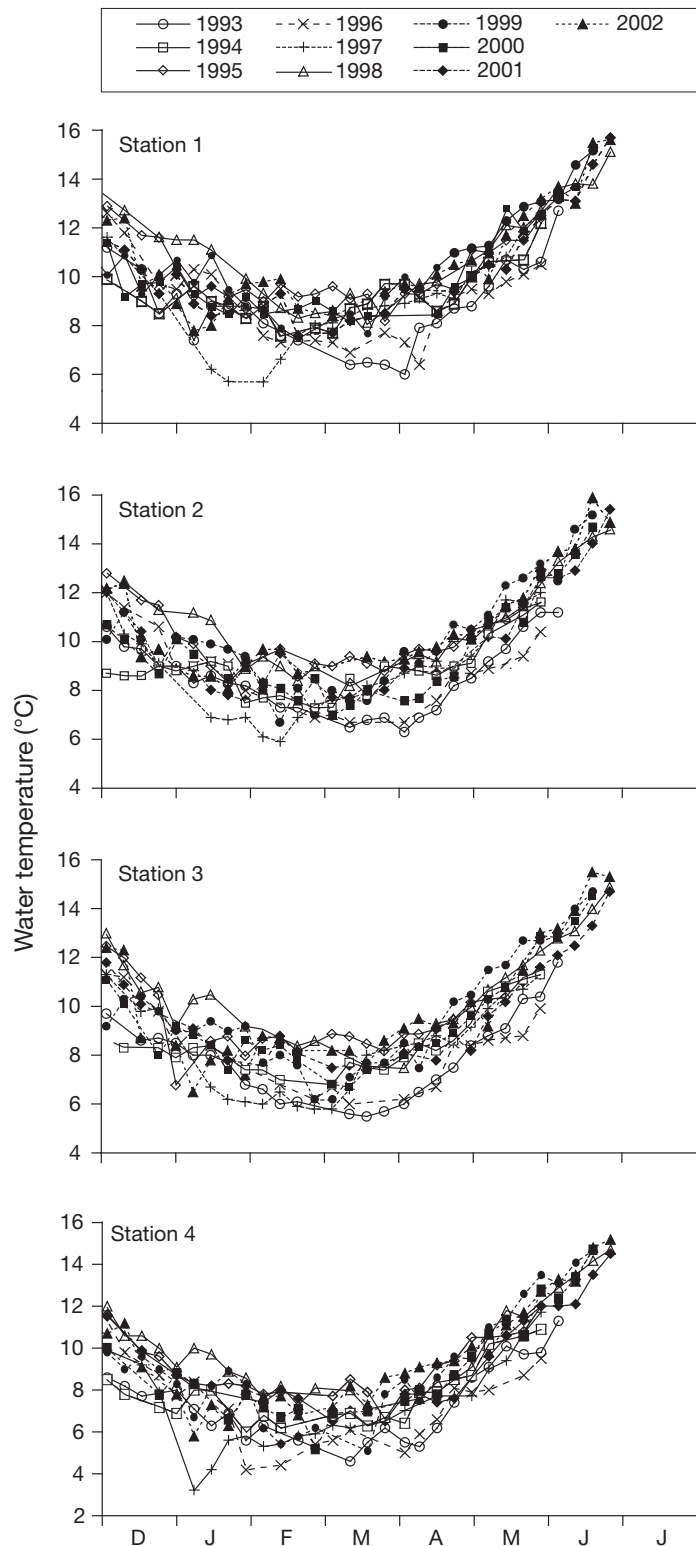


Fig. 2. Mean weekly water temperatures (°C) at the 4 stations on the transect from the spawning area towards the Marsdiep inlet for 1993 to 2002. Data are based on NOAA satellite images. For exact positions of the stations see van der Veer & Witte (1999, their Fig. 1a, Table 1).

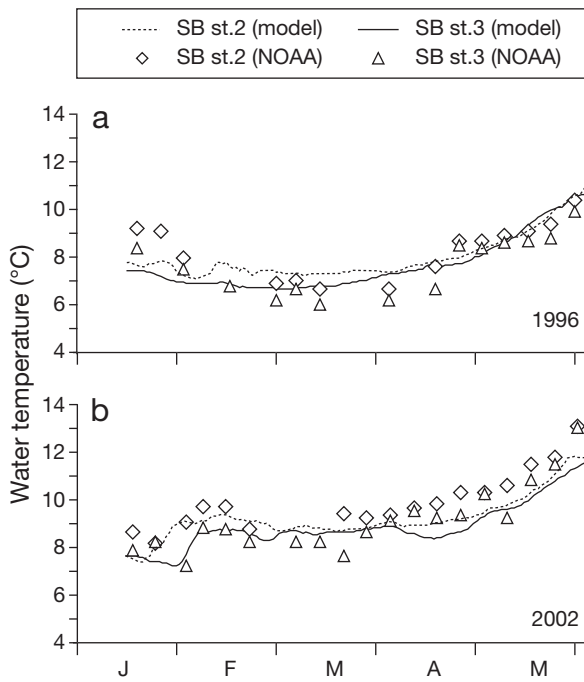


Fig. 3. Comparison of water temperature estimates from NOAA satellite images of Stns 2 and 3 (see Fig. 1a) with model predictions from the Delft3D-FLOW hydrodynamic model (Erfteemeijer et al. 2009) for (a) 1996 and (b) 2002

Overall, there was no relationship between the water supply at Balgzand (weekly amounts at high water) and the index of larval supply. However, within most years the trend was positive, and in several years, including the exceptionally strong year class of 1996, the relationship was negative (data not shown). Addi-

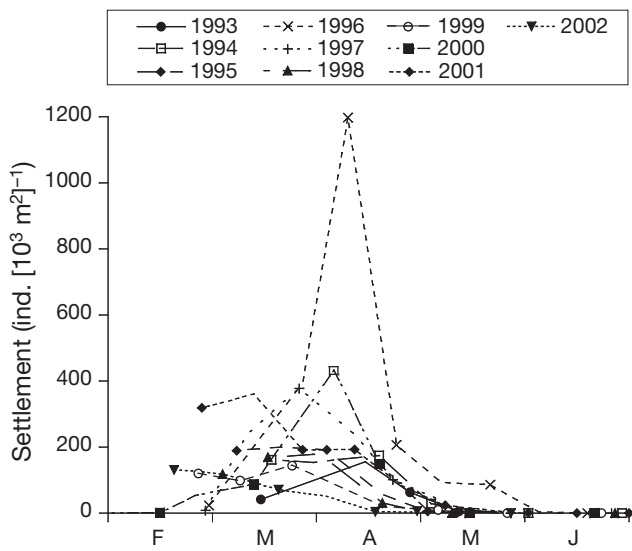


Fig. 4. *Pleuronectes platessa*. Settlement patterns of plaice larvae at the Balgzand, based on densities of just-settled individuals (≤ 15 mm) following van der Veer (1986)

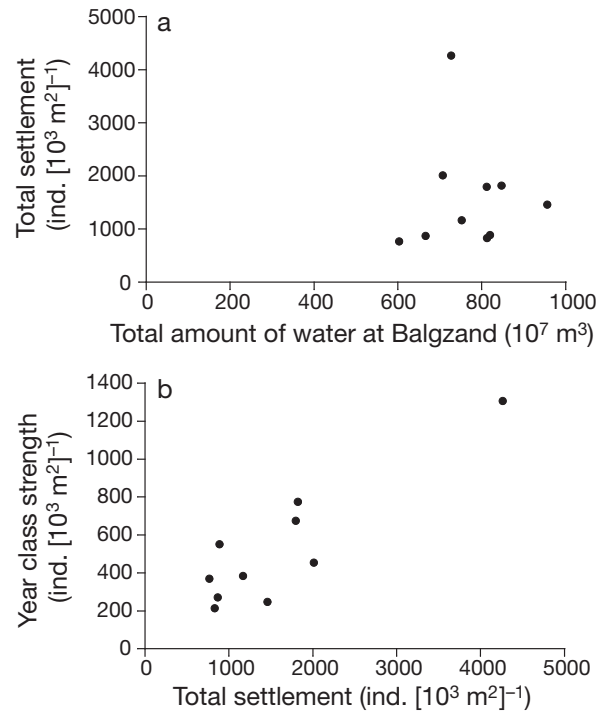


Fig. 5. *Pleuronectes platessa*. (a) Relationship between total amount of water at high water at Balgzand tidal flats during settlement in spring and total amount of settling plaice larvae for 1993–2002. (b) Relationship between total amount of settling plaice larvae and peak abundance of 0-group plaice, used as an index of year-class strength for 1993–2002

tionally, for the whole period of larval immigration, no relationship was found between total amount of water at Balgzand and total settlement of larvae ($r_s = 0.20$, $n = 10$, $p > 0.25$ [ns]) (Fig. 5a). Year-class strength of 0-group plaice was significantly correlated with total larval settlement ($r_s = 0.71$, $n = 10$, $p < 0.05$) (Fig. 5b).

Weekly mean larval stage duration varied over the years between 36 and 57 d. In some years (1994, 1995, 1996, 2002), weekly mean larval stage duration decreased over the period of larval immigration, in other years there was no clear trend (1998, 1999, 2000) and in 1997 and 2001 it increased over time (Fig. 6a). The GLS was applied to model the relationship between duration and timing of settlement and year. The interaction between timing of settlement and year was significant ($L = 42.31$, $df = 8$, $p < 0.001$), which means that the relationship between duration and timing of settlement changed over the years. The correlation between residuals from the same year (θ) was -0.19 . No significant relationship was found between mean larval stage duration and year class strength ($r_s = -0.15$, $n = 9$, $p = 0.62$) (Fig. 6b).

The relationship between larval development time and temperature was calculated from published values (see Bolle et al. 2009). The relationship takes the

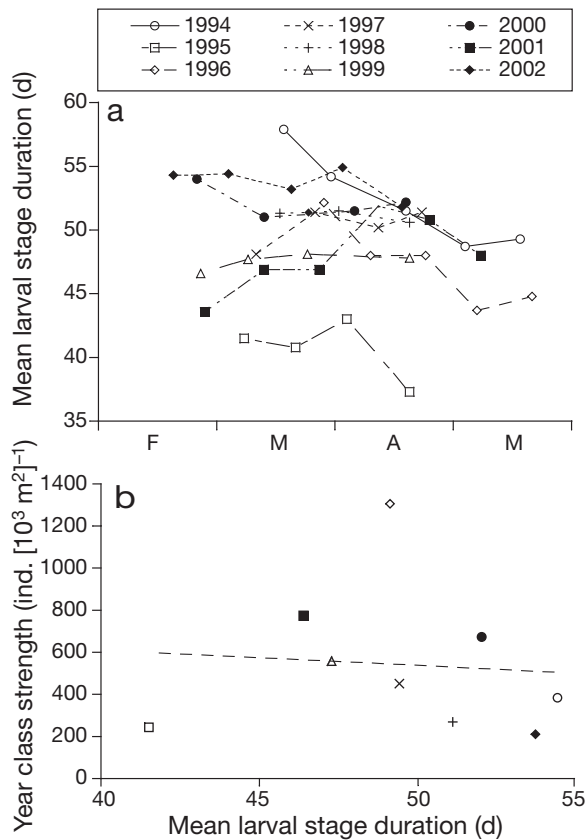


Fig. 6. *Pleuronectes platessa*. (a) Mean larval stage duration (d) during the period of larval immigration in the western Wadden Sea from 1994 to 2002. (b) Relationship between mean larval stage duration (d) and year-class strength of plaice (ind. $[10^3 \text{ m}^2]^{-1}$) at Balgzand from 1994 to 2002

form of $\ln(D) = 5.0 - 0.15T$, where D is larval stage duration in days and T is temperature in $^{\circ}\text{C}$. This relationship was largely driven by the experimental data published by Talbot (1977). Due to experimental bias, it is unclear to what extent this relationship reflects maximum development rates. For the field data, median water temperature during the pelagic period fluctuated between 6 and 9°C , and the resulting calculated larval stage duration according to the model varied between a prediction of 40 and 55 d (Fig. 7a). The GLS showed that the interaction between temperature and year was not significant, and therefore the interaction was dropped from the model. Estimated parameters are given in Table 1. Note that temperature has a negative effect. The likelihood ratio test was applied to calculate probabilities for the categorical variable year ($L = 30.37$, $df = 8$, $p < 0.001$) and for temperature ($L = 8.21$, $df = 1$, $p = 0.004$). The correlation between residuals from the same year was $r_s = 0.32$. The observed decline in larval stage duration with temperature was much less than expected based in literature data (Fig. 7a).

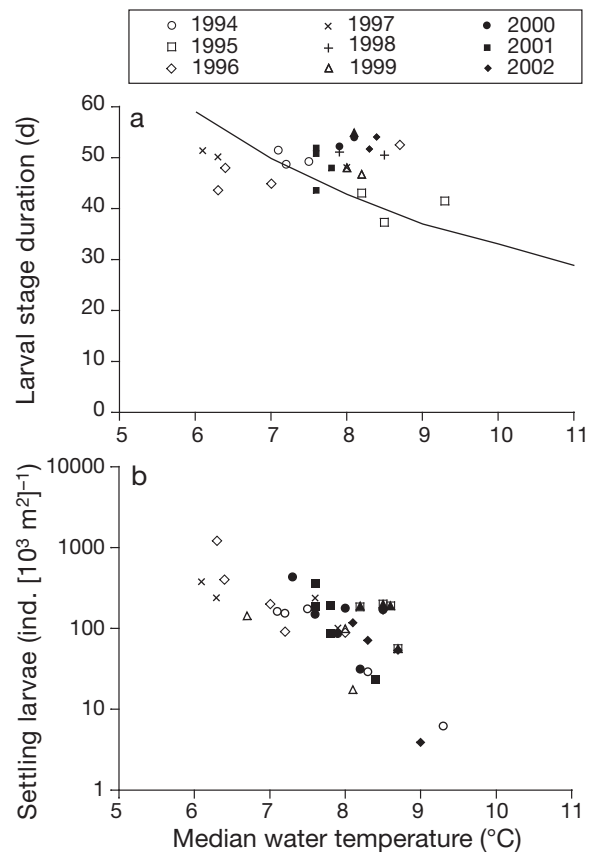


Fig. 7. *Pleuronectes platessa*. Relationship between median water temperature ($^{\circ}\text{C}$) during larval plaice drift and mean larval stage duration (d). Line indicates development based on literature data on development rates compiled by Bolle et al. (2009). (b) Relationship between median water temperature ($^{\circ}\text{C}$) during larval drift and number of settling plaice larvae at the Balgzand intertidal

The number of settling larvae varied from almost zero to <1000 ind. $(10^3 \text{ m}^2)^{-1}$ (Fig. 7b). The GLS was also applied to model the number of settling plaice larvae in relation to median temperature and year. The residual correlation within a year was $r_s = -0.24$. In all models the effect of temperature was negative. The absence of a trend in median temperature during the larval immigration period ($r_s = 0.24$, $n = 40$, $p > 0.05$ [ns]) indicated that this relationship was not generated by collinearity between median temperature and time (day number). The likelihood ratio test indicated that the interaction between temperature and year was significant ($L = 20.71$ $df = 8$, $p = 0.008$), though a sequential F -test indicated that it was not significant ($p = 0.154$, Table 2). Differences between these 2 tests may be due to the small sample size, and indicates the caution needed for interpretation of the interaction. When the interaction term was removed, both main terms temperature and year were significant (as can be inferred from 2 likelihood ratio tests, results not shown).

Table 1. *Pleuronectes platessa*. Generalised least squares model of larval stage duration, (Duration) = Median temperature (Temp) × Year

	Value	SE	t	p
(Intercept)	66.22376	5.678556	11.662077	0.0000
Temp	-1.76444	0.683446	-2.581678	0.0158
factor(Year)1995	-10.57605	2.627723	-4.024796	0.0004
factor(Year)1996	-6.50799	2.619544	-2.484399	0.0197
factor(Year)1997	-3.64182	2.666072	-1.365985	0.1836
factor(Year)1998	-0.56323	2.680774	-0.210101	0.8352
factor(Year)1999	-4.94738	2.676725	-1.848294	0.0760
factor(Year)2000	-1.24738	2.676725	-0.466008	0.6451
factor(Year)2001	-3.49058	2.546450	-1.370762	0.1822
factor(Year)2002	2.39306	2.630532	0.909725	0.3713

Table 2. *Pleuronectes platessa*. Generalised least squares model of number of settling larvae, (Lar) = Median temperature(Temp) × Year. Results from a sequential ANOVA (df = 18)

	df	F	p
(Intercept)	1	28554.299	<0.0001
Temp	1	319.570	<0.0001
factor(Year)	8	18.984	<0.0001
Temp:factor(Year)	8	1.750	0.1543

DISCUSSION

Importance of hydrographic variability

Differences in water circulation patterns were thought to affect the strength and direction of residual currents and thereby the success of larval transport (e.g. Rijnsdorp et al. 1995, van der Veer et al. 2000a, Bolle et al. 2009). Hydrodynamic transport models highlighted the importance of interannual variability in weather conditions for transport of plaice in the open sea (Nielsen et al. 1998, van der Veer et al. 1998, Bolle et al. 2009). However, the observed patterns of larval immigration do not appear to be related to variability in duration of larval transport. The length of larval stage varied within and among years, but without any clear pattern in relation to environmental variables. Larval stage duration depends on the combined effect of food and temperature conditions. NOAA satellite images have shown that interannual variability in the temperature conditions during the period of larval drift is small (van der Veer & Witte 1999). In the absence of significant temperature variation, the observed variation in the duration of the larval period, in combination with observed differences in hydrodynamic circulation (Nielsen et al. 1998, van der Veer et al. 1998, Bolle et al. 2009), imply that from year to year the immigrating larvae at the Marsdiep inlet originate from different spawning areas. Beverton & Lee (1965) observed that

the drift of plaice in the Southern Bight of the North Sea differed substantially in 2 contrasting years. In the cold year of 1963, the main patch of plaice larvae occurred north of the Wadden Sea and appeared to have 'missed' the Marsdiep inlet. Rijnsdorp et al. (1985) observed that Marsdiep immigration sometimes seems to be bimodal, and concluded that the first mode was not related to the Southern Bight spawning grounds, but rather to the eastern English Channel spawning. Hovenkamp (1991), observing differences in larval stage duration, concluded that the various cohorts entering

the western Wadden Sea originated from different spawning grounds. This fits the observation that plaice eggs are not restricted to well-defined spawning areas but spread out over the entire southern part of the North Sea (van der Land 1991) and suggests that connectivity between spawning grounds and nursery areas in the southern North Sea can vary from year to year, and that the high success rate, as indicated by successful recruitment, is made possible by the extensive nursery areas around the North Sea.

The observed relationship between nursery size and juvenile abundance (so-called nursery size hypothesis; Rijnsdorp et al. 1992, van der Veer et al. 2000a) stresses the importance of the international Wadden Sea as nursery area for plaice (Zijlstra 1972, van Beek et al. 1989). Intuitively, with increasing nursery size, connectivity between spawning and nursery areas will be stronger, because the chances for larvae to arrive at some part of the nursery increase. The observed relationship between year-class strength of settling plaice at Balgzand and subsequent recruitment (van der Veer, 1986), stresses the importance of the Wadden Sea. Larvae have passed suitable nursery areas outside the Wadden Sea in the coastal zone before arriving at Balgzand and, furthermore, they also can settle at neighbouring intertidal areas. In this respect it is unclear whether (and to what extent) Balgzand receives all the initial settlement, or whether larvae that settled in the coastal zone are redistributed. The fact that larvae can withstand starvation for days (Creutzberg et al. 1978) only increases their flexibility with respect to selecting settlement areas and might explain the lack of relationship between water supply at Balgzand and the amount of settling larvae.

Predation versus starvation

Temperature conditions during the egg and larval stages directly dictate the potential growth rate of indi-

viduals. During development in the egg and yolk-sac stage, internal energy reserves provide the essential energy sources; however, as soon as feeding starts external sources become essential. For plaice in the Southern Bight, appendicularians (especially *Oikopleura dioica*) are the main external food source (Shelbourne 1962, Ryland 1964). Fast growth is considered to be of importance because predation is often size-selective (Ebenman & Persson 1988, van der Veer et al. 1997) and hence the risk of mortality is inversely related to the size of an individual fish (Cushing 1974, Rothschild 1986). As a result, prey is considered to pass through a sequence of size-selective predation windows whereby growth directly determines the transit time (Houde 1989).

Larval stage duration showed a slight decrease with increasing temperature, a result in line with the observations by Hovenkamp & Witte (1991). However, the decrease in observed duration with increasing temperature was much smaller than the relationship compiled from literature sources (Bolle et al. 2009). This might suggest increasing food limitation during the pelagic stage with increasing temperature, resulting in slower growth and a longer larval period. Whether only reduced growth or also starvation occurs is unclear. Empty stomachs are often found in immigrating larvae (H. W. van der Veer unpubl. data) and settlement is thought to be induced by feeding of starving larvae (Creutzberg et al. 1978). However, in the late larval stages, plaice larvae can survive for a few weeks without food at 9°C (Blaxter & Ehrlich 1974).

The reconstructions of the larval stage duration suggest that in all years the transit time of developing plaice in the Southern Bight through the sequence of size-selective predation windows was more or less the same and the increase in growth potential at higher temperature was not likely achieved because of an increased food limitation. It is unclear whether this also holds true for developing larvae originating from other spawning areas. Southern Bight plaice larvae experience relatively constant temperature conditions during development due to the fact that it takes place in the plume of English Channel water (van der Veer & Witte 1999). For developing larvae from other spawning areas, temperature conditions might be more variable. In a previous study (Hovenkamp & Witte 1991) an inverse relationship was observed between growth and water temperature for the youngest stages; however, unlike the present study, the temperature history of the larvae was not reconstructed using NOAA satellite images.

Temperature conditions also directly affect predation pressure. Sprat and herring have been identified as predators on plaice eggs (Hansen 1955, Pommeranz 1981, Daan et al. 1985, Last 1989, Rijnsdorp & Jaworski

1990, Ellis & Nash 1997), cod and herring are able to prey on plaice larvae (Fuiman & Batty 1994) and the coelenterates *Aurelia aurita* and *Pleurobrachia pileus* are known predators of the late larval stages (Bailey & Batty 1984, van der Veer 1985). Predator activity is related to temperature, and predation pressure in general increases exponentially with increasing water temperature (see for overview Willmer et al. 2000). Normally, the positive effect of temperature on growth counteracts the negative effect on daily mortality rate so that stage-specific cumulative mortality rates of post-larval fish are independent of temperature (Pepin 1991). However, Southern Bight plaice might deviate from this pattern because mean larval stage duration did not show a clear pattern with reconstructed temperature conditions. Therefore, for Southern Bight plaice, it might be expected that stage-specific cumulative mortality rates will increase with increasing temperature during drift. The observed inverse relationship between number of immigrating larvae and temperature conditions during drift, both within and among years, fits with such a mechanism. The findings of the present study are in line with the results for Irish Sea plaice, where starvation and predation have been identified as key factors in early life survival (Fox et al. 2007). Selective mortality will certainly determine the estimates of larval stage duration, since these are observed from samples of survivors at settlement. Selective survival of the fastest growing larvae would act to dampen any observed relationship between larval stage duration and temperature, and in warmer years the larvae from more distant spawning areas may reach metamorphosis before they reach the Balgzand nursery ground.

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