



Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British Isles)

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ABSTRACT: For species with extended spawning seasons, short periods of beneficial conditions often lead to disproportionate survival of sub-sets of the offspring. This has been demonstrated for freshwater fish and for marine pelagic species, but has been less frequently tested for other teleost groups. Using offshore plankton surveys, we constructed egg production curves for plaice *Pleuronectes platessa* L. in the eastern Irish Sea. Data from 5 yr showed that spawning began sometime before January and was completed by the end of April. Over these years the timing of peak spawning varied between mid-February and mid-March. In 2001, 2002 and 2003, we also sampled post-settlement plaice from inshore nursery grounds. Otolith micro-increment analyses and temperature-dependent egg development rates were used to back-calculate the birth dates of the settled fish. By June, immigration to the nursery grounds was largely completed and the shape of the reconstructed birth-date distributions corresponded closely to the relevant egg production curves. In contrast to many other studies, there was little evidence for significantly disproportionate survival of specific portions of the egg production curve between spawning and the recently post-settled stages. Such a survival pattern could be generated by a gradual switch from starvation to predation as the principal cause of larval mortality as the spawning season progressed.

KEY WORDS: Plaice · Eggs · Larvae · Spawning · Survival · Selective mortality · Otolith microstructure

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INTRODUCTION

Unravelling the factors controlling year-class strength in fish populations remains a major challenge. Although the average relationships between spawning biomass (as a proxy for egg production) and recruitment for different taxonomic groups (clupeoids, gadoids, etc.) are well established (Goodwin et al. 2006), the causative mechanisms remain poorly defined. Since year-class strength is usually considered to be determined during the first year of life, special emphasis is given to processes affecting survival of the egg, as well as larval and early juvenile stages (Rijnsdorp et al. 1995, Hyder & Nash 1998).

Using otolith analysis to back-calculate the hatch dates of juvenile fish, the relative survival of cohorts can be assessed by comparing the abundance of juveniles with the relevant portion of egg production (Anderson 1995). Such studies have provided support for 'birth-date selection', i.e. in any 1 yr there are periods of beneficial conditions that allow disproportionate survival of a sub-set of the eggs spawned. Beneficial conditions might include an absence of predators (Bailey & Houde 1989), the availability of suitable prey (Cushing 1990), or periods with suitable oceanographic conditions (Lasker 1981). There has, however, been little consistency in the portions of spawning output re-

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ported to show enhanced survival—some studies have reported higher relative survival of the early spawned offspring (Cargnelli & Gross 1996, Lapolla & Buckley 2005), others of those spawned later (Hoenig et al. 1990, Fossum & Moksness 1993, Wright & Bailey 1996), whilst multi-year studies have often reported inter-annual variability (Methot 1983, Hovenkamp 1991, Wright & Gibb 2005). These differing patterns have been taken as evidence that batch spawning over an extended time has evolved as a 'bet-hedging' strategy in response to the inherent uncertainty in the timing of suitable conditions for egg and larval survival (Winemiller & Rose 1993). Few studies have reported constant survivorship of offspring throughout the spawning season—although see Moksness & Fossum (1992) for an example.

Plaice *Pleuronectes platessa* are a common north European flatfish, which spawn offshore in water >20 m deep in the early months of the year. Eggs and larvae can take up to 3 mo to complete development during which time they are transported towards coastal nursery grounds where they settle following metamorphosis (Gibson 1999). There have been numerous studies on the post-settlement ecology of plaice, but, since the 1960s, the planktonic stages have received relatively less attention (Beverton & Iles 1992a). This is unfortunate since enhanced survival during these planktonic stages is a pre-requisite for the production of strong year-classes (van der Veer et al. 2000). In the present study, ichthyoplankton surveys were used to determine the timing and location of plaice egg production in the eastern Irish Sea. Later in the year, beach surveys around the whole eastern Irish Sea coast were used to assess the abundance and spatial distribution of post-settlement survivors. We estimated the birth dates of survivors, from analyses of otoliths and temperature-dependent egg development rates, and examined how relative survivorship changed over each spawning season.

MATERIALS AND METHODS

Ichthyoplankton surveys. Ichthyoplankton surveys were used to assess egg production in 1995, 2000, 2001, 2002 and 2003. In 1995 and 2000, the aim was to produce an estimate of plaice *Pleuronectes platessa* spawning stock biomass by the annual egg production method and the whole Irish Sea was surveyed (Armstrong et al. 2001, Arm-

strong & Dickey-Collas 2002). In subsequent years, sampling was concentrated on the eastern spawning grounds (east of 4° 45' W), with the intention of linking egg production to subsequent settlement. The general sampling grid is shown in Fig. 1 (exact positions varied slightly from cruise to cruise depending on weather conditions), and the survey dates are shown in Fig. 2. Plankton sampling protocols for 1995 and 2000 have been fully described in Armstrong et al. (2001) and Armstrong & Dickey-Collas (2002) and for subsequent years followed the methods in Fox et al. (2006). Briefly, ichthyoplankton samples were collected using high-speed plankton samplers deployed in double-oblique tows (Nash et al. 1998). Plaice eggs were identified according to Russell (1976) and assigned to developmental stages (Ryland & Nichols 1975). The abundance of Stage I eggs was converted to daily production ($\text{no. m}^{-2} \text{d}^{-1}$) using the temperature-dependent stage duration model given in Fox et al. (2003). Generalised additive models (GAMs) were fitted to the egg production data for each year (Fox et al. 2000a). The GAMs were then used to predict daily egg production over the eastern or western Irish Sea using latitude, longitude and day of

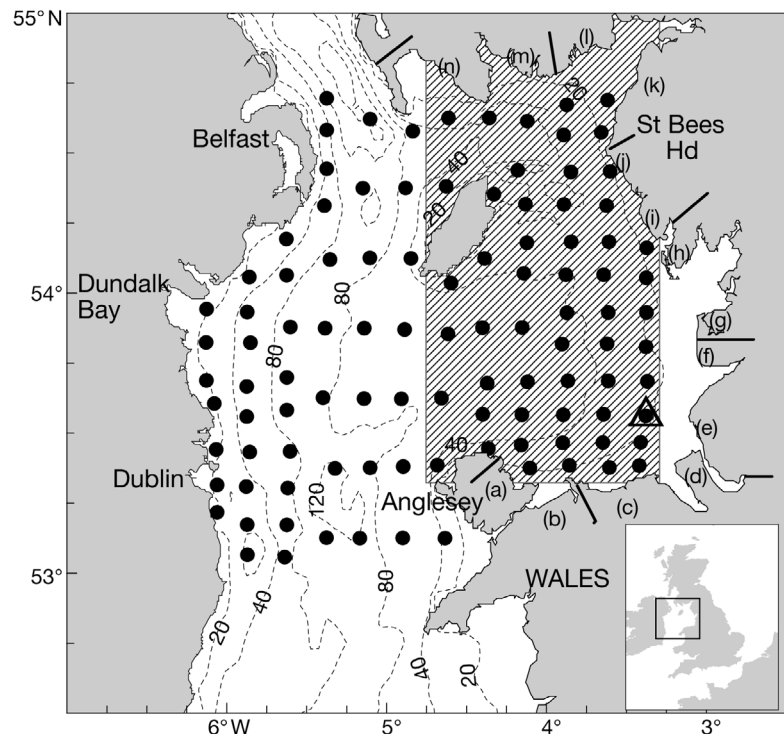


Fig. 1. Sampling locations for the plankton surveys (●) and beach surveys (a–n)—hatched area shows region covered by surveys in 2001, 2002 and 2003. Beach survey sites—Zone 1: (a) Red Wharf Bay, (b) Penmaenmawr; Zone 2: (c) Rhyl, (d) West Kirby; Zone 3: (e) Southport, (f) Blackpool; Zone 4: (g) Heysham, (h) Aldingham; Zone 5: (i) Silcroft, (j) Seascale; Zone 6: (k) Beckfoot, (l) Sandyhills; Zone 7: (m) Gatehouse of Fleet, (n) Auchenmalg. Solid lines indicate the limits of each zone; triangle indicates the location of the Cefas Liverpool Bay SmartBuoy

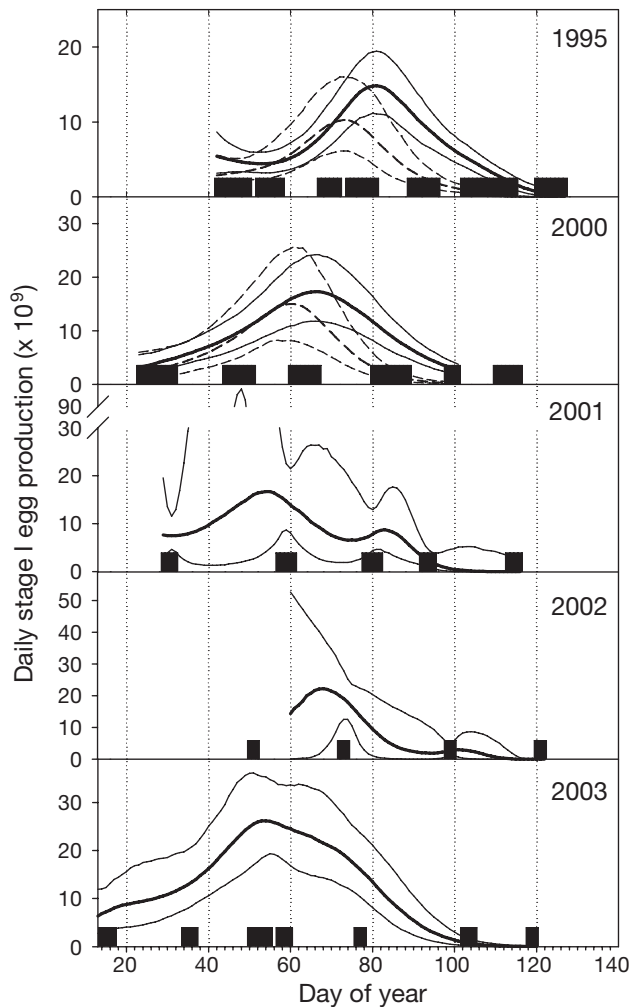


Fig. 2. *Pleuronectes platessa*. Egg production curves for 1995, 2000, 2001, 2002 and 2003. Thick line: median production; thinner lines: 0.025 and 0.975 percentiles of 1000 bootstrap iterations of the generalised additive model (GAM); solid lines are data for the eastern Irish Sea; dashed lines are data for the western Irish Sea (1995 and 2000 only); solid horizontal bars show the plankton cruise coverage

year (DOY) as predictive covariates. Confidence intervals were generated from 1000 iteration bootstraps of the residuals of the fitted models.

Environmental data from plankton surveys. Temperature and salinity were measured at each plankton station using salinity–temperature–depth (STD) probes mounted on the plankton samplers. Estimates of temperatures experienced by plaice eggs were necessary to determine the duration of the egg stage (Fox et al. 2003). For the eastern Irish Sea, integrated water column temperatures from stations along longitude $3^{\circ}48'W$ were selected coincident with the highest plaice egg concentrations (Fox et al. 2000a). For the western Irish Sea, temperatures recorded at all stations

west of longitude $5^{\circ}30'W$ were used (Fox et al. 2000a). The average water column temperature for each plankton survey, weighted by the abundance of Stage I plaice eggs, was also computed. For early 2002, no offshore temperature data were available, as plankton sampling was disrupted by poor weather. During this period we assumed that water temperatures would have been similar to the earliest available measurements for that year. For 2003, additional continuous, near-surface temperature records were available from a mooring located at the eastern edge of the survey grid (Fig. 1). Regressions fitted to the temperature data allowed estimation of the average water temperature experienced by plaice eggs in each year.

Juvenile plaice surveys. During the last 2 wk of May and June 2001, 2002 and 2003, beam trawl surveys were undertaken to assess the abundance of settled juveniles on potential plaice nursery grounds around the eastern Irish Sea coast (Fig. 1). Sampling was undertaken during daylight at low water since recently settled '0' group plaice are concentrated close to the surf-line at these times (Gibson et al. 2002). Sampling sites were accessed using all-terrain vehicles (ATVs), since at low water some of the sampling locations were several kilometres from the high-water mark. In May 2001, 1.5 m beam trawls were used, but were found to be too light for the terrain and were changed to heavier, 2 m beam trawls in June 2001. The 2 m trawls were used in all the subsequent beach surveys. Each 1.5 m trawl was fitted with a single tickler chain and 10 mm stretched mesh in the belly and the cod end; the 2 m trawls were each fitted with 4 tickler chains, 14 mm stretched mesh bodies and 10 mm stretched mesh cod-end liners. At each site 4 replicate tows were made orthogonal to the shore. The beam-trawls were walked out 100 m, the distance being determined using a marked tow-rope. At a few sites (e.g. Silecroft) the water deepened rapidly so tows were made at an angle of 45° to the shore. In all cases the beam-trawl was then positioned to avoid towing over disturbed ground and towed ashore using the ATVs at 5 km h^{-1} .

The catch from each tow was immediately sorted, and all juvenile flatfish transferred into a foil envelope and frozen in a liquid-nitrogen dry shipper. On return to the laboratory, samples were thawed and individual fish identified and measured (total length). '0' group plaice were identified on the basis of length frequency plots and examination of the otoliths from a subset of the larger plaice for the presence of the first annual increment. Numbers of settled '0' group plaice were converted to abundance m^{-2} assuming the beam-trawls were 30% efficient (Nash & Geffen 2000). No correction was applied for potential differences in catch efficiency between the 1.5 m beam trawl (used in May 2001) and the 2 m beam trawls (used in all other surveys), nor were corrections made for size-selective

gear efficiency. Because the catches of settled plaice in different tows within a sampling zone were often right-skewed, mean and 95% confidence limits for plaice density by sampling zone were computed using a 1000 iteration bootstrap (S-Plus, Insightful). The mean densities for each zone were then raised by the area of non-rocky seabed (km²) between the mean low water mark and the 2 m depth contour (in May and June, post-settlement plaice are found from the water's edge to a depth of 1 to 2 m (Gibson et al. 2002). Seabed areas were computed by planimetry of hydrographic charts. Charted information is not readily available for Morecambe Bay (Zone 4) or the Solway Estuary (Zone 6), so best estimates were obtained as described in Fox et al. (2006).

Determination of birth and settlement dates of juvenile plaice. Birth and settlement dates of individual juvenile plaice were estimated as below:

$$\text{DOY}_{\text{settled}} = \text{DOY}_{\text{sampled}} - \text{OTO}_{\text{outer}} \quad (1)$$

$$\text{DOY}_{\text{hatched}} = \text{DOY}_{\text{sampled}} - \text{OTO}_{\text{outer}} - \text{OTO}_{\text{inter}} - \text{OTO}_{\text{inner}} \quad (2)$$

$$\text{DOY}_{\text{spawned}} = \text{DOY}_{\text{hatched}} - \text{EGG} \quad (3)$$

where DOY is day of year, OTO is the number of microincrements in the inner, intermediate, or outer region of the otolith, and EGG is the duration of the egg stage estimated from temperature-dependent development rates given in Fox et al. (2003) and using the estimated average temperature for the DOY_{hatched} in the relevant year.

For each sampling zone, approximately 30 post-settlement plaice were sub-sampled from the total catch proportional to the overall size distribution. The sagittal otoliths were extracted from these specimens using fine dissecting needles and mounted on microscope cover slips using Crystalbond (Aremco Products). The otoliths were hand-ground to the core using aluminium oxide lapping film (30 and 9 µm; South Bay Technology) and polished using a Picador, supra-white polishing block (Evans Lapidary). The otoliths were then examined using transmitted light on a compound microscope linked to an image analysis system. Three readers independently enumerated micro-structures. Three areas of the otolith were counted separately: an inner region corresponding to the pelagic period, an intermediate region corresponding to settlement, and an outer region corresponding to the time since settlement. The inner area extended from the hatch ring (Karakiri et al. 1989) to the first accessory growth centre, and increments were counted using a ×100 oil immersion objective. The intermediate region extended from the first accessory growth centre to the end of the accessory growth structures, and increments lying between the accessory growth structures were counted using a ×20 objective.

The outer region extended from the first increment completely surrounding all the accessory growth structures to the edge of the otolith. Outer region increments were counted using a ×20 objective. Counts for these areas were accepted if all 3 readings lay within a range of 12% of the mean. In some cases it was difficult to count the number of increments immediately adjacent to the hatch ring. For these otoliths, the distance across this section was measured and an estimate was made of the number of un-resolved rings assuming that average ring width in this area was 0.5 µm (based on scanning electron microscope preparations, comparison with light microscope measurements and results reported in Hovenkamp 1991).

For each otolith, total increment counts were calculated using the mean of the 3 readers' counts. Total increment counts were taken as an estimate of the number of days between hatching and capture on the assumption that the micro-increments had been deposited daily (Karakiri et al. 1989).

To compensate for the problem of cumulative post-settlement mortality when estimating true hatch-date distributions, the total numbers for each age group of juvenile plaice collected were raised as:

$$M = \exp(z \times \text{OI}) \quad (4)$$

where M is the mortality correction, z is the daily instantaneous mortality rate, and OI is increment counts in the outer region of the otolith. Because we only had 2 sets of beach surveys (May and June) we could not directly estimate post-settlement mortality for each sampling zone, so we assumed an average rate of 0.018 d⁻¹ from Table 8 in Beverton & Iles (1992a).

Although plaice were sub-sampled for otolith analyses on a length-stratified basis, otoliths from larger fish tended to be harder to prepare and count. In some cases this resulted in under-representation of the larger size groups. Results were weighted to correct for any bias introduced. The results for each zone were then raised so that the total corresponded to the estimated population of '0' group plaice for that zone. Finally, the distributions of spawning and settlement dates for '0' group plaice across the whole eastern Irish Sea were derived by summation across all the sampling zones.

Survivor analyses. Following Anderson (1995) we computed relative fitness functions comparing the hatch date distribution of juvenile plaice from the beach surveys in June (S_2) with that year's egg production (S_1). Relative fitness was estimated as:

$$f(z) = \frac{S_1}{S_2} \left[\frac{h(z)}{1-h(z)} \right] \quad (5)$$

where the conditional probability that a fish with birth date z was caught in the sample of survivors,

given that it was caught in either the before-selection or after-selection group is:

$$h(z) = \frac{S_2(z)}{S_2(z) + S_1(z)} \quad (6)$$

The relative fitness function has a mean of approximately 1. Values of the index in the range (0 to 1) indicated that cohorts were under-represented in the surviving population relative to egg production, whilst values >1 indicated that cohorts were over-represented. To estimate confidence intervals for the fitness index, we recomputed $f(z)$ on 1000 bootstraps of the underlying otolith data. The 0.025, 0.5 and 0.975 percentiles of the 1000 $f(z)$ estimates, where z is daily, were then smoothed by Loess using a smoothing interval of 0.15.

Table 1. *Pleuronectes platessa*. Total numbers of Stage I eggs produced (TEP, $\times 10^{11}$) in the eastern and western (where data were available) Irish Sea estimated by 1000 bootstraps of fitted generalised additive models (GAMs)

Year	Eastern Irish Sea				Western Irish Sea			
	Mean	Percentile			Mean	Percentile		
		0.025	0.5	0.975		0.025	0.5	0.975
1995 ^a	5.75	4.77	5.73	6.79	3.37	2.31	3.33	4.73
2000 ^a	7.65	5.75	7.59	9.85	5.10	3.21	4.97	7.39
2001	8.02	5.75	7.59	9.85				
2002 ^b	6.70	1.86	6.22	13.98				
2003	13.10	10.20	13.00	16.20				

^aUsing a histogram method, total Stage I egg production was estimated at ca. 6×10^{11} in the eastern Irish Sea and at 4×10^{11} in the western Irish Sea in 1995 (Armstrong et al. 2001) and at ca. 10×10^{11} in the eastern Irish Sea and at 7×10^{11} in the western Irish Sea in 2000 — before egg mortality correction (Armstrong & Dickey-Collas 2002). The differences with GAM-based estimates are due to the different egg development rates and integration methods used

^bAssumes symmetrical spawning around DOY 68 to cover missing data at the start of the year caused by poor weather

RESULTS

Plankton surveys

In all years, spawning of *Pleuronectes platessa* probably began in December, prior to the first ichthyoplankton cruises¹. In 1995, peak spawning occurred around mid-March, but in more recent years the peak occurred up to 20 d earlier (Fig. 2). In years with good temporal and spatial survey coverage (1995, 2000 and 2003), 95% confidence intervals around mean daily egg production were relatively tight, but, in years when sampling was disrupted by poor weather (2001 and 2002), precision was much lower (Fig. 2, Table 1). The total quantity of Stage I eggs produced increased between 1995 and 2003 (Table 1). It should be noted that these estimates have not been corrected for any egg mortality experienced between spawning and sampling (see Dickey-Collas et al. [2003] for a discussion of the problems associated with applying such corrections). In 2002, weather conditions were particularly poor and largely prevented sampling in January and February. We therefore assumed that egg production was symmetrical about the peak (DOY 68) in that year. Based on years where data were available for

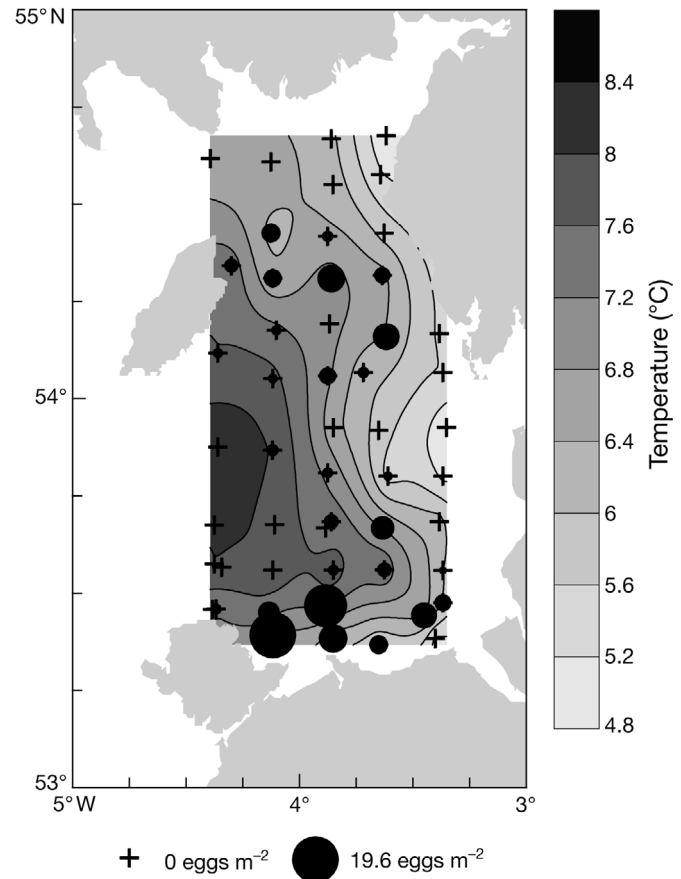


Fig. 3. *Pleuronectes platessa*. Distribution of Stage I eggs and water column temperature for the first plankton survey in 2001 (29 January to 1 February). Area of the solid circles is proportional to number of plaice eggs m^{-2} sea surface

¹The raw data from the ichthyoplankton surveys have been published in Fox et al. (1997), Bunn & Fox (2004) and Bunn et al. (2004) and are available on request. Analyses of the 1995 and 2000 results in relation to the estimation of plaice spawning-stock biomass have been published in Armstrong et al. (2001) and Armstrong & Dickey-Collas (2002)

both the western and eastern Irish Sea, spawning in the east contributed 64 and 60% of the total Irish Sea plaice egg production (1995 and 2000, respectively). In the western Irish Sea, plaice spawned close to the Irish coast from Dundalk Bay to Dublin (Fox et al. 2000a). In the eastern Irish Sea, the main concentrations of eggs occurred off the North Wales coast, although they were found as far north as the Isle of Man (Fig. 3).

Thermal stratification was only observed in STD profiles collected during April and May. For all other months, the maximum difference between surface and bottom temperatures was $<1^{\circ}\text{C}$, indicating that the water column was generally well mixed. However, strong horizontal gradients in water column temperature were found in the eastern Irish Sea moving offshore, particularly in January and February (Fig. 3, present study; Bunn et al. 2004). Temperatures in the eastern Irish Sea tended to be cooler than in the west at times when plaice eggs were abundant (Fig. 4). Estimated water temperatures experienced by plaice eggs in the eastern Irish Sea were in the range from 6 to 7°C in 1995, 2000 and 2001, but waters were slightly warmer (6.5 to 8°C) in 2002 and 2003. These relatively narrow temperature ranges resulted in estimated egg incubation periods of between 13 and 18 d.

Beach surveys

Bimodal size distributions of settled plaice were evident in some sampling zones, particularly in 2002 (Figs. 5 to 7). By examining the otoliths of a subset of the larger fish it was confirmed that they had been spawned the previous year. This information was used to set size limits separating '0' and '1' group fish (Table 2). Using these size limits, the distribution patterns of settled '0' group plaice were similar in 2001, 2002 and 2003, with the highest mean densities being found in Zones 1 (North Wales) and 4 (Morecambe Bay; Table 3). In 2001 and 2003, plaice densities increased between the May and June surveys in Zone 1 and Zone 6 (Solway Estuary), indicating that plaice were still immigrating into these nursery grounds. However, this was not the case for the other zone,

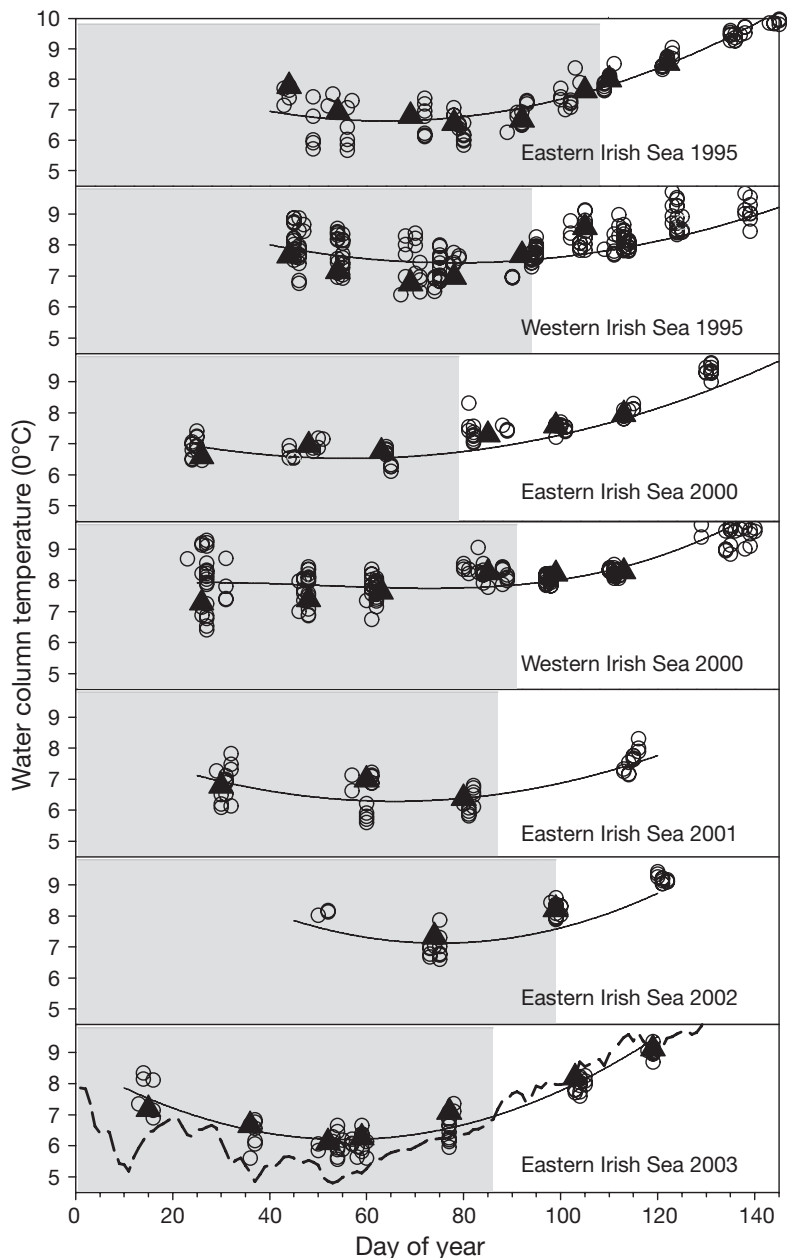


Fig. 4. Water column temperatures in the Irish Sea. ○: integrated water column temperatures from the $3^{\circ}48'W$ longitudinal transect and from west of longitude $5^{\circ}30'W$; ▲: mean water column temperature for each plankton survey weighted by the abundance of Stage I plaice eggs; solid line shows cubic polynomial regression; dashed line shows the continuous surface water temperature record from the Cefas Liverpool Bay SmartBuoy (2003 only); grey background indicates the time over which 95% of plaice egg production occurred

where plaice were most abundant (Zone 4). In 2002, overall settlement levels were lower, but similar distribution patterns were noted. The balance of immigration against mortality was slightly different, resulting in a small increase in the total number of settled plaice in the eastern Irish Sea between the May and June

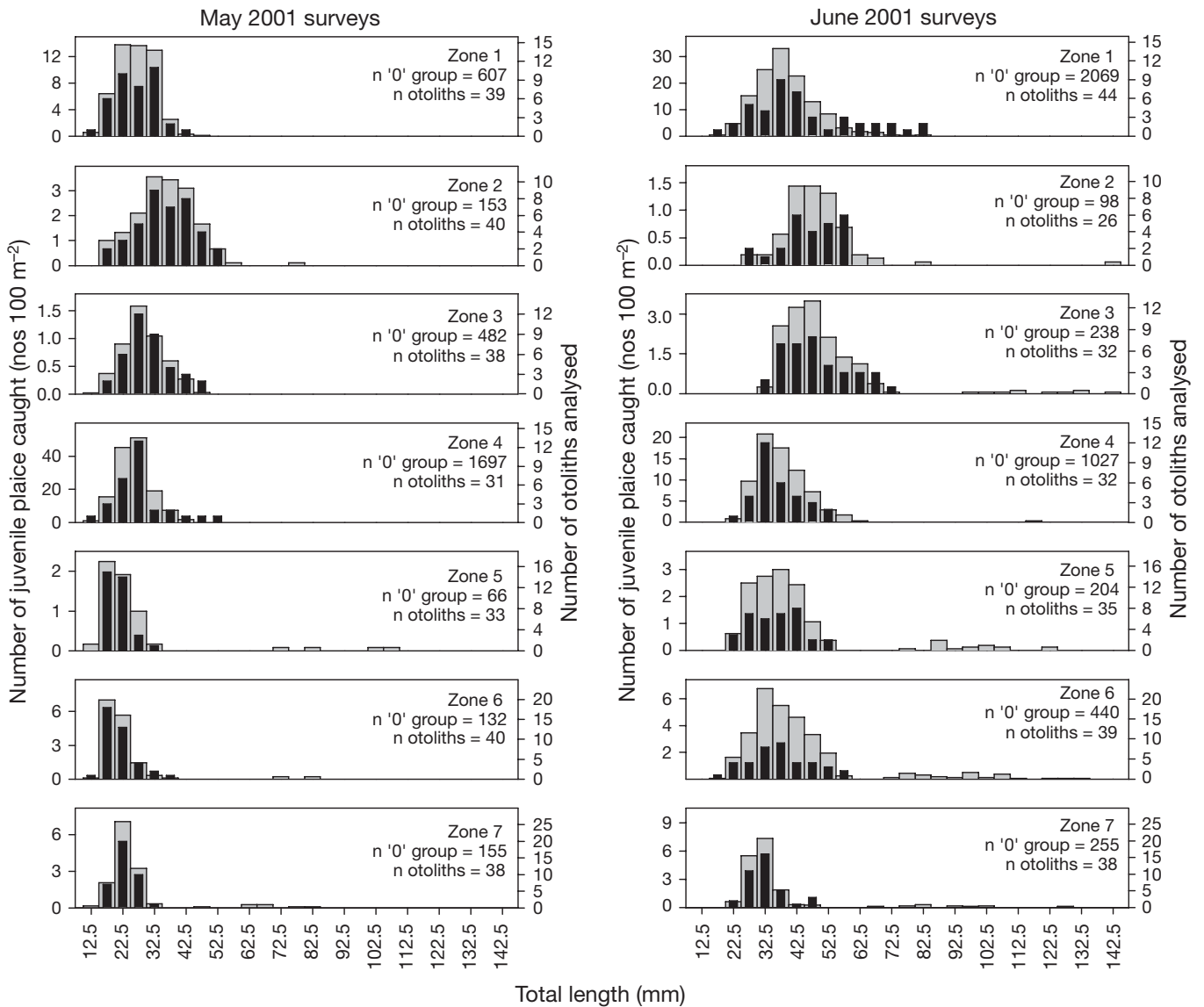


Fig. 5. *Pleuronectes platessa*. Length frequencies for settled fish caught in 2001 by sampling zone. Grey bars: total number of plaice caught, by 5 mm length groups standardised to 100 m² of swept area. Black bars: number of otoliths analysed

Table 2. *Pleuronectes platessa*. Upper size limits separating '0' group and '1' group plaice (total length in mm) caught during the 2001, 2002 and 2003 beach surveys. NA: not available

Zone	2001		2002		2003	
	May	June	May	June	May	June
1	50	85	55	75	65	75
2	60	70	55	75	60	75
3	50	75	45	75	65	75
4	55	80	55	70	60	75
5	40	55	NA	50	45	65
6	40	60	40	65	60	70
7	35	50	40	50	45	60

surveys. Regardless of year, by June, Zones 4 and 6 were each estimated to hold about one-third of the total population, whilst Zone 1 held between 12 and 23%. The remaining sampling zones combined held <20% of the overall population.

Over the whole study, otoliths from 1618 juvenile plaice were extracted and analysed. Of these, 92 were rejected after failing the inter-reader comparison described in the 'Materials and methods'. Around 50% of the otoliths could not be counted right into the hatch ring; the average distance measured over which increments were estimated was 3.5 µm. Acceptable micro-increment counts were obtained from the otoliths of at least thirty '0' group plaice from each sampling zone

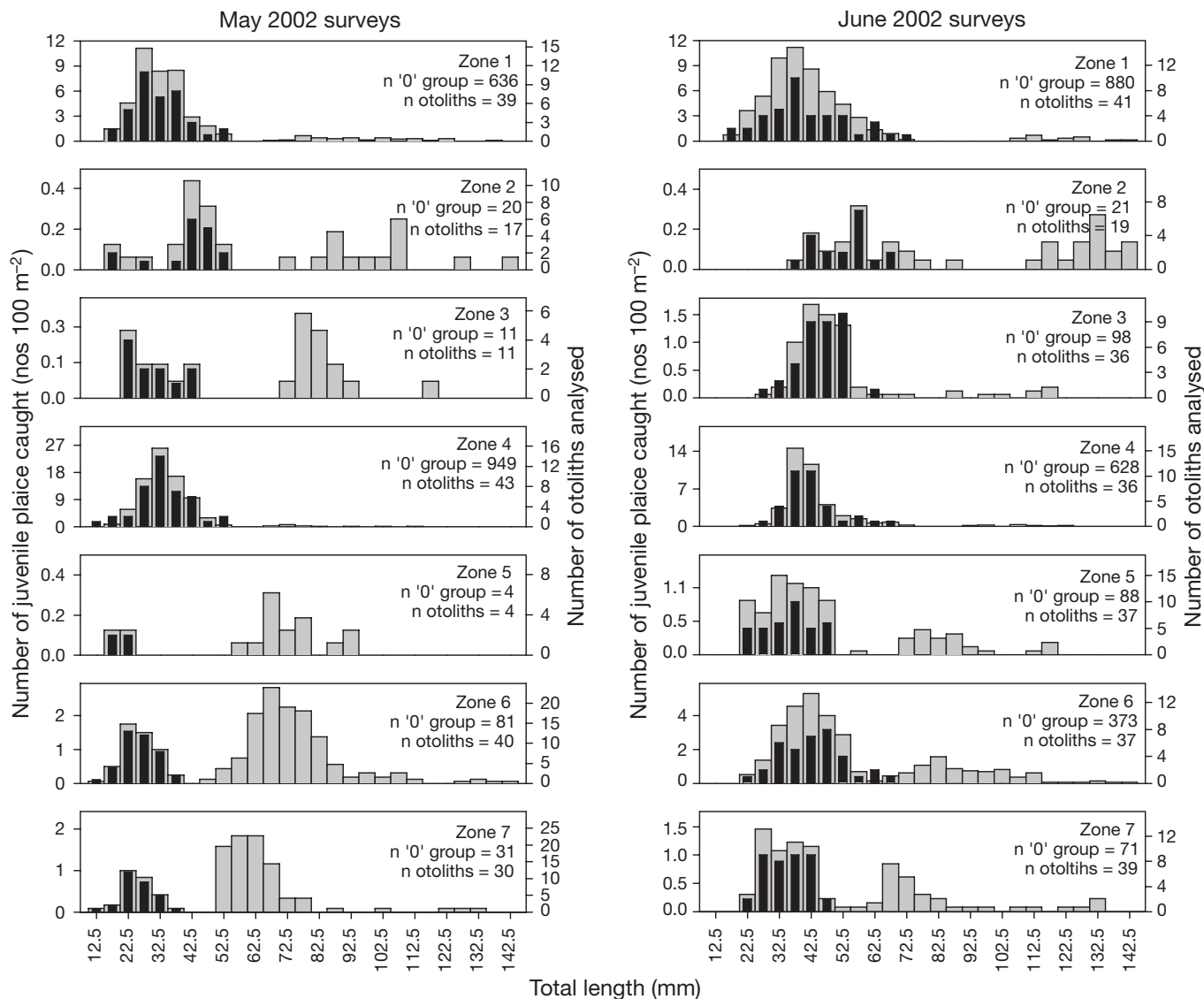


Fig. 6. *Pleuronectes platessa*. Length frequencies for settled fish caught in 2002 by sampling zone. Further details as in Fig. 5

(except for sampling zones where <30 juvenile plaice were caught), adequately representing the length frequency of the '0' group fish caught in that zone (Figs. 5 to 7). An exception was Zone 2 from June 2002, where all the otoliths from fish >65 mm total length failed to give satisfactory results. This was corrected by in-filling the gap using the overall relationship between fish length and increment counts for that zone (no significant year effect on the relationship between fish length and the number of increments in the outer part of the otolith (ANCOVA $p = 0.05$)—data were pooled across years; Table 4). The number of larval increments in the otoliths varied between 31 and 55 (mean \pm SD: 42 ± 4 , $n = 1526$), whilst the number of increments in the intermediate region of the otolith was quite variable, with a range from 10 to 37.

Based on changes in plaice abundance and length frequencies we assumed that immigration was largely completed by the time of the second set of beach surveys in June (Table 3, Figs. 5 to 7). By then there were significant differences in the lengths of settled plaice between the sampling zones (Kruskal-Wallis tests of zone effect on data by survey, all tests $p < 0.05$). The general pattern was similar between years, with fish in Zone 2 and Zone 3 tending to be larger than in the other sampling zones (Fig. 8). For Zone 2 this appeared to be due to earlier settlement, rather than higher post-settlement growth rates (Fig. 8, Table 4). Fish caught in Zone 2 had also been spawned earlier, compared with those in other zones, and this was consistent for all 3 years (Fig. 8). For fish in Zone 3, differences in DOY spawned and settled were less obvious,

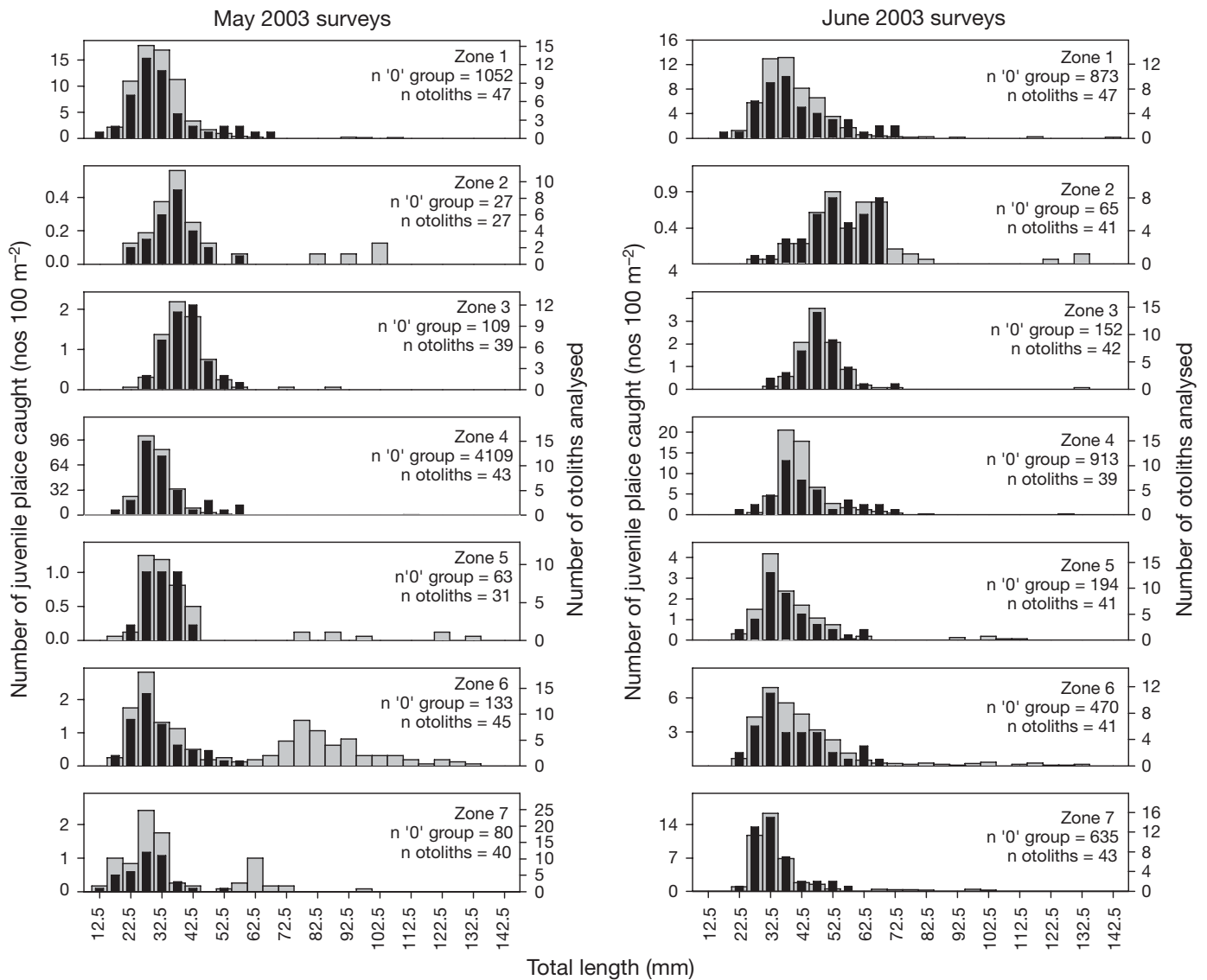


Fig. 7. *Pleuronectes platessa*. Length frequencies for settled fish caught in 2003 by sampling zone. Further details as in Fig. 5

and higher post-settlement growth rates might have been responsible for their larger size in the June surveys (Table 4). Zones 2 and 3, however, contributed <10% of the overall settled plaice population (Table 3), and, for the major nursery grounds (Zones 1, 4 and 6), differences in median DOY spawned were relatively small (<15 d).

Selection by birth date in the early life stages

In the May surveys, the birth-date distributions for the settled plaice were skewed towards pre-peak spawning (Fig. 9). This appeared to be the result of incomplete immigration to the nursery grounds, since, by June, the birth-date distributions more

closely reflected the egg production curves (Fig. 9). In all years the birth-date distribution was truncated, so that survivors from eggs spawned at the end of the season were missing. This missing fraction represented 8% of the overall egg production in 2001 and 2002 and 3% in 2003. Correcting the data for post-settlement mortality resulted in relatively minor differences in the shape of the hatch-date curves compared with uncorrected data (Fig. 9). Relative fitness curves computed from the June survey data (corrected for post-settlement mortality) showed little evidence of exceptionally strong survival of fish spawned in any particular period (Fig. 10). Only at the very end of the spawning season did the 95% confidence intervals from the bootstrap of $f(z)$ exclude $f(z) = 1$.

Table 3. *Pleuronectes platessa*. Field observations on distribution of settled 0-group plaice around the eastern Irish Sea in 2001, 2002, and 2003. Values in parentheses are 2.5% limit, mean, and 97.5% limit, respectively

Zone	Area (km ²)	Density of recently settled plaice (no. m ⁻²)		Estimated total population of settled plaice (million)		Percentage of total (%)	
		May	June	May	June	May	June
2001							
1	19.7	(0.88, 1.69, 2.69)	(3.10, 4.22, 5.55)	(17.3, 33.3, 53.0)	(61.1, 83.1, 109.3)	7.5	23.4
2	61.8	(0.11, 0.56, 1.66)	(0.09, 0.20, 0.39)	(6.8, 34.6, 102.6)	(5.6, 12.4, 24.1)	7.8	3.5
3	34.8	(0.54, 1.33, 3.62)	(0.30, 0.48, 0.78)	(18.8, 46.6, 126.0)	(10.4, 17.1, 27.1)	10.5	4.8
4	58.0	(2.65, 4.72, 9.97)	(1.20, 2.44, 6.13)	(153.7, 273.8, 578.3)	(69.6, 141.5, 355.5)	61.5	39.8
5	14.2	(0.09, 0.18, 0.27)	(0.21, 0.32, 0.45)	(1.3, 2.6, 3.8)	(3.0, 6.1, 6.4)	0.6	1.7
6	90.9	(0.20, 0.49, 0.60)	(0.67, 0.91, 1.52)	(18.2, 44.5, 54.5)	(60.9, 82.7, 138.2)	10.0	23.3
7	20.9	(0.14, 0.45, 1.27)	(0.34, 0.61, 0.89)	(2.9, 9.4, 26.5)	(7.1, 12.7, 18.6)	2.1	3.5
Total	300.3			(219.0, 444.8, 944.7)	(217.7, 355.6, 679.2)	100.0	100.0
2002							
1	19.7	(0.67, 1.32, 2.14)	(1.44, 1.83, 2.42)	(13.2, 26.0, 42.2)	(28.4, 36.1, 47.7)	14.2	18.3
2	61.8	(0.02, 0.04, 0.07)	(0.02, 0.06, 0.15)	(1.2, 2.5, 4.3)	(1.2, 3.7, 9.3)	1.4	1.9
3	34.8	(0.00, 0.02, 0.07)	(0.16, 0.20, 0.28)	(0, 0.7, 2.4)	(5.6, 7.0, 9.7)	0.4	3.5
4	58.0	(1.54, 2.35, 3.54)	(0.99, 1.31, 2.02)	(89.3, 136.3, 205.3)	(57.4, 76.0, 117.2)	74.5	38.5
5	14.2	(0.00, 0.01, 0.03)	(0.13, 0.18, 0.31)	(0, 0.1, 0.4)	(1.8, 2.6, 4.4)	0.1	1.3
6	90.9	(0.09, 0.17, 0.30)	(0.44, 0.76, 1.26)	(8.2, 15.5, 27.3)	(40.0, 69.1, 114.5)	8.4	35.1
7	20.9	(0.03, 0.09, 0.16)	(0.06, 0.15, 0.27)	(0.6, 1.9, 3.3)	(1.3, 3.1, 5.6)	1.0	1.6
Total	300.3			(112.6, 182.9, 285.3)	(135.7, 197.5, 308.4)	100.0	100.0
2003							
1	19.7	(1.49, 2.19, 3.08)	(1.24, 1.82, 2.30)	(29.4, 43.1, 60.7)	(24.4, 35.9, 45.3)	7.4	12.5
2	1.8	(0.02, 0.06, 0.11)	(0.06, 0.14, 0.22)	(1.2, 3.7, 6.8)	(3.7, 8.7, 13.6)	0.6	3.0
3	34.8	(0.17, 0.23, 0.29)	(0.13, 0.32, 0.58)	(5.9, 8.0, 10.1)	(4.5, 11.1, 20.2)	1.4	3.9
4	58.0	(5.09, 8.62, 17.20)	(1.40, 1.89, 3.08)	(295.2, 500.0, 997.6)	(81.2, 109.6, 178.6)	85.2	38.1
5	14.2	(0.08, 0.13, 0.18)	(0.28, 0.40, 0.57)	(1.1, 1.8, 2.6)	(4.0, 5.7, 8.1)	0.3	2.0
6	90.9	(0.15, 0.28, 0.45)	(0.77, 0.98, 1.25)	(13.6, 25.5, 40.9)	(70.0, 89.1, 113.6)	4.3	31.0
7	20.9	(0.08, 0.22, 0.35)	(0.78, 1.32, 1.74)	(1.7, 4.6, 7.3)	(16.3, 27.6, 36.4)	0.8	9.6
Total	300.3			(348.2, 586.7, 1125.9)	(204.1, 287.6, 415.8)	100.0	100.0

DISCUSSION

Studies on the immigration of plaice *Pleuronectes platessa* to nursery grounds have shown that immigration often occurs in 'pulses' (Rijnsdorp et al. 1985, van der Veer 1986, Al-Hossaini et al. 1989, Hovenkamp 1991) with some inter-annual variability in the timing of arrival (Riley & Corlett 1966, Lockwood 1974, Zijlstra et al. 1982, Al-Hossaini et al. 1989, van der Veer et al. 2000, Wennhage & Pihl 2001). Although many of these studies included frequent sampling of the settling fish, only Hovenkamp (1991) was able to directly compare reconstructed hatch-dates with measured egg production. In the other studies, inter-annual differences in timing of immigration and 'pulses' of arrival could have been caused by variable inter-cohort survival, but these patterns could also be due to other factors, such as variability in the timing of spawning (Lange & Greve 1997), temperature effects on egg and larval development (Hyder & Nash 1998), or varying egg and larval transport (Nielsen et al. 1998, van der Veer et al. 1998).

Our results, in which egg production was directly assessed and coupled with large-scale coverage of

potential nursery grounds, suggested that mortality between spawning and early post-settlement at the population level was relatively constant within season. Such a pattern has only been reported in one other study, Moksness & Fossum (1992). Whilst variable birth-date selection is readily accounted for by the patchiness of predators and prey in the environment (Winemiller & Rose 1993), constant survival is more difficult to explain.

Starvation and predation are generally thought to be the major causes of mortality of pre-recruit stages of fish, and the intensity of both these factors probably varies during the year (Cushing 1996). Other factors such as mechanical damage and extremes of temperature or salinity appear to contribute little to egg and larval mortality, although the roles of pollution, disease and parasites have not been thoroughly investigated (Bunn et al. 2000). In the Irish Sea most plaice hatch well before the spring zooplankton bloom (Prestidge & Taylor 1995), so starvation could be a significant factor. However, there has been little new evidence for starvation of plaice larvae in the field since Shelbourne (1957) reported finding patches of poor-condition lar-

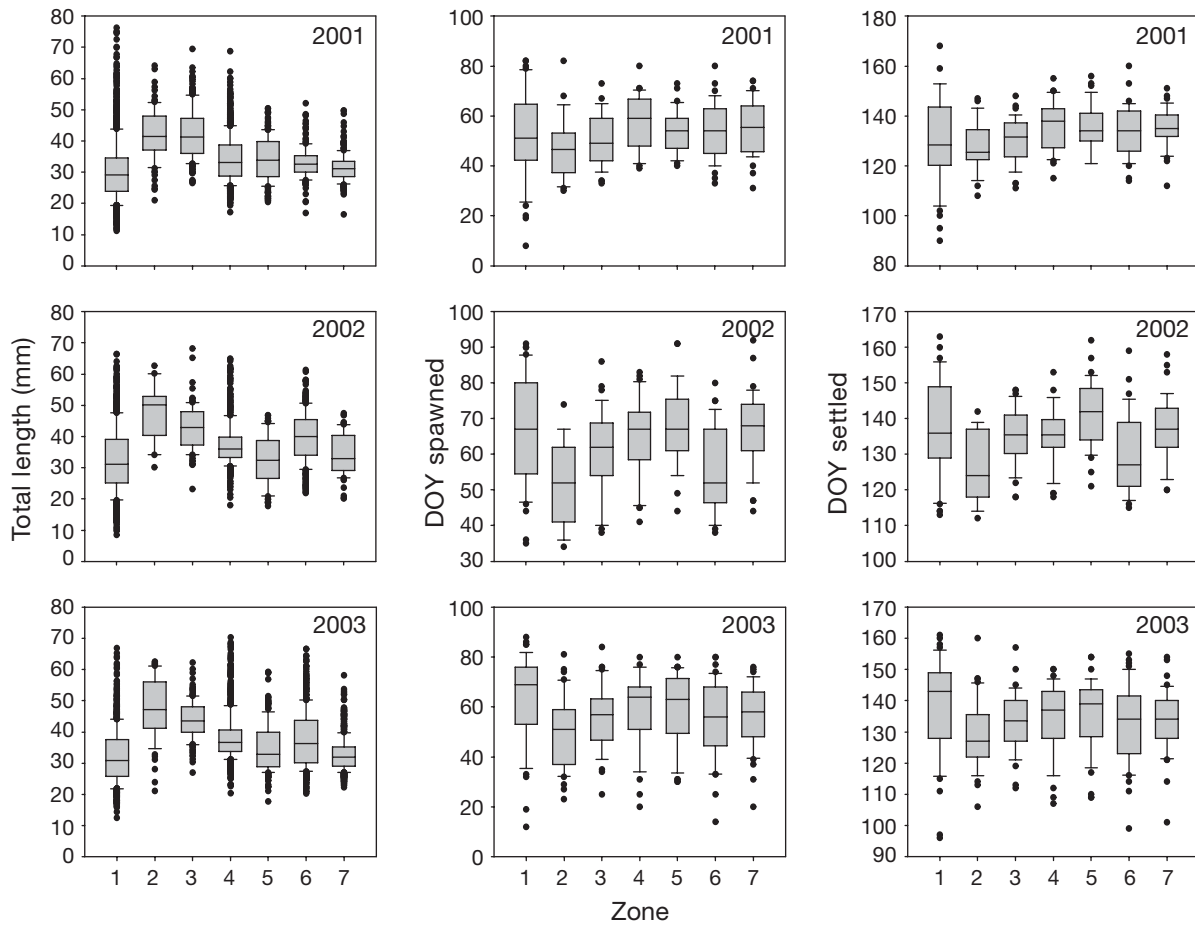


Fig. 8. *Pleuronectes platessa*. Total lengths, estimated day of year (DOY) of spawning and estimated DOY of completion of settlement for '0' group fish caught in June beach surveys. Length data were corrected to a common date of the first survey in June of each year using zone-specific growth regressions; horizontal bars indicate medians; boxes indicate the upper and lower quartiles; dots indicate outliers

vae in the North Sea. In laboratory experiments plaice larvae appear rather resistant to starvation as the point-of-no return at temperatures of 9°C is between 10 and 18 d (Blaxter & Ehrlich 1974). Even if larvae are not actually killed by starvation, shortage of prey, along with lower temperatures early in the season, will reduce larval growth rates, increasing the time that they are exposed to predators (Cushing 1990). Predation on plaice eggs and larvae by fish such as herring *Clupea harengus* and sprat *Sprattus sprattus* and invertebrates such as the ctenophore *Pleurobrachia pileus* is well documented (Pommeranz 1981, Daan et al. 1985, van der Veer 1985, Ellis & Nash 1997, Segers et al. 2007). Since the abundance and activity rates of many of these predators are linked to temperature, predation intensity might be expected to increase through the spring and early summer (van der Veer & Sadee 1984, Hovenkamp 1991). However, increasing temperatures will also lead to increased plaice larval growth rates potentially countering the increased pre-

dation risk. This could generate a relatively constant level of mortality throughout the spawning season — in line with our results.

Our overall conclusions rely on several assumptions. Firstly, there must not have been any substantial im-

Table 4. *Pleuronectes platessa*. Regressions of total fish length (TL) against number of increments in the outer region of the otolith (OI) by sampling zone (all years pooled). All regressions were highly significant ($p < 0.001$)

Zone	Regression	n	r ²
1	TL = 14.06 + 0.72 × OI	258	0.83
2	TL = 18.03 + 0.71 × OI	174	0.82
3	TL = 18.51 + 0.69 × OI	210	0.75
4	TL = 14.99 + 0.72 × OI	229	0.84
5	TL = 16.41 + 0.61 × OI	183	0.82
6	TL = 14.60 + 0.68 × OI	242	0.80
7	TL = 16.92 + 0.53 × OI	230	0.74

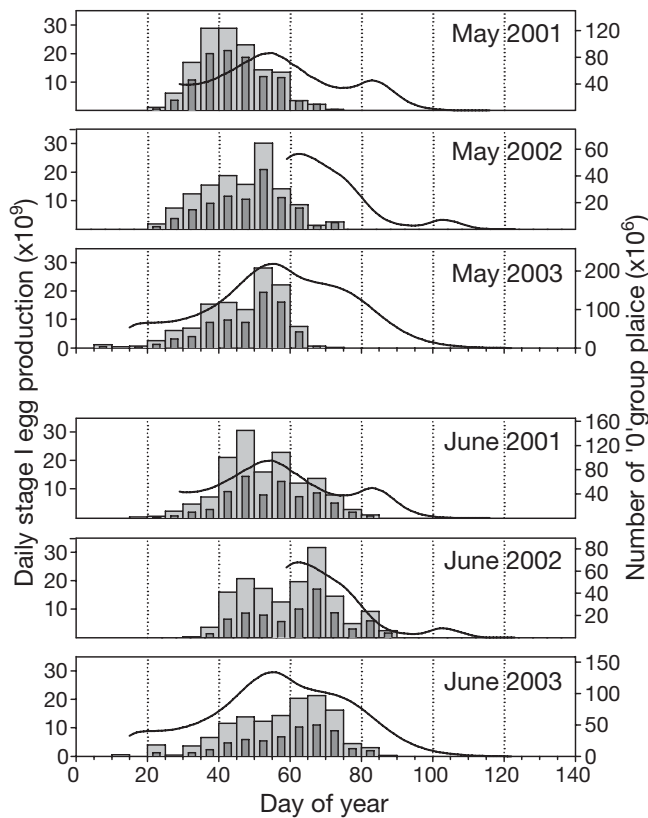


Fig. 9. *Pleuronectes platessa*. Comparisons of plaice birth-date distributions and egg production curves for 2001 to 2003. Solid line indicates egg production; dark grey bars: birth-date distributions of the entire eastern Irish Sea settled '0' group plaice population; light grey bars: birth-date distributions corrected for post-settlement mortality

migration of larvae from spawning grounds outside of the study area. Particle tracking models have demonstrated an efficient transport of plaice eggs and larvae from the eastern Irish Sea spawning grounds to adjacent nursery grounds (Fox et al. 2006). At the start of this study we therefore assumed that spawning and nursery grounds in the western and eastern Irish Sea operated as independent units. More recent modelling has shown that a portion of the eggs spawned in the west may, in fact, reach nursery grounds around the eastern Irish Sea (van der Molen et al. 2007). However, since total egg production in the western Irish Sea is lower than in the east (Table 1), only about 10% of plaice settling in the eastern Irish Sea would have come from the west.

Secondly, we assumed that we could interpret otolith micro-increments to give high precision estimates of age. Karakiri & von Westernhagen (1989) reported daily increment deposition in plaice larvae when the rearing temperature was $>5^{\circ}\text{C}$. The increments were also wide enough to be visible using light microscopy.

We estimated that the temperatures experienced by plaice larvae in our study were $>6^{\circ}\text{C}$ (Fig. 4), so we expect that the increments would have been sufficiently wide to be resolved. Our estimates of larval duration were also consistent with the values of between 42 and 59 quoted by Al-Hossaini et al. (1989) for Irish Sea plaice. Larval increment counts appear to be substantially lower in Irish Sea plaice compared with those from the North Sea, where the range is 50 to 82 (Karakiri et al. 1989, 1991). This probably reflects warmer temperatures in the Irish Sea, which would lead to shorter larval durations (Fox et al. 2000b). In the accessory growth structures, we observed fewer, wider increments as noted by Al-Hossaini et al. (1989). We assumed that increment counts in the clearer regions between accessory structures reflected the total time between metamorphosis and completion of settlement (Modin et al. 1996). Because these increments are more difficult to interpret, estimates of the time taken to complete settlement may be less accurate than for other periods (Nash & Geffen 2005). Several studies have validated post-settlement micro-increment formation, although their interpretation can be compli-

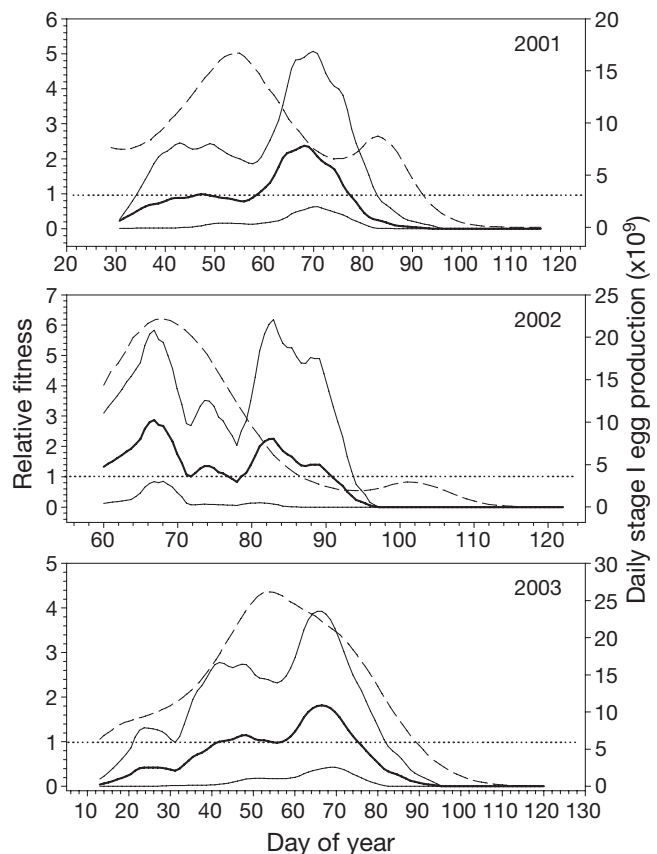


Fig. 10. *Pleuronectes platessa*. Relative fitness (thick lines) $\pm 95\%$ confidence band (thin lines) between egg production and estimated birth dates of settled '0' group plaice in June 2001 to 2003. Dashed line indicates estimated egg production

cated by the presence of sub-daily increments and checks that may be caused by tidal rhythms affecting feeding and growth (Al-Hossaini & Pitcher 1988, Karakiri et al. 1989, Berhahn 1990, Geffen & Nash 1995).

Thirdly, we assumed that we could correct the DOY reconstructions for the effects of post-settlement mortality by assuming a fixed mortality rate of 0.018 d^{-1} . This is the currently accepted average derived from various nursery grounds and covering a range of plaice sizes (Iles & Beverton 1991, Beverton & Iles 1992b), but mortality rates for recently settled plaice may be higher, e.g. 0.025 to 0.073 d^{-1} in Red Wharf Bay (Al-Hossaini et al. 1989) or 0.017 to 0.086 d^{-1} in Port Erin Bay (Nash & Geffen 2000). Furthermore, there could have been some variation in mortality rates between nursery grounds. Difficulties in measuring post-larval mortality remain a problem with survival analysis when it has not been possible to sample the fish during settlement itself. It is probably only practical to conduct such intensive sampling over small areas, but these may then not be representative of the dynamics of adult populations which recruit from many nursery grounds (Nash 1998, van der Veer & Witte 1999).

Ideally, survival studies need to be carried out over regional spatial scales and over many years in order to include environmental and year-class extremes. The 3 years studied, 2001 to 2003, resulted in average year-classes of Irish Sea plaice (assessed at Age 2, available at www.ices.dk) and were also not extreme in terms of multi-decadal records of Irish Sea temperatures and winds. Different patterns of birth-date selection might well be observed for years producing exceptionally strong year-classes, but detecting this would require a much longer term study (van der Veer et al. 2000).

Acknowledgements. This research was funded by Defra under Project M0423. The authors acknowledge the dedication of the officers and crews of the RVs 'Prince Madog', 'Corystes', 'Cirolana' and 'Lough Foyle' and of the FV 'Resolute'; W. Rowlands, S. Beggs, K. Sullivan, M. Smith, M. Shaw, C. Burt, R. Taylor, R. Clarke, L. Adlam, M. Andrews and J. Kennedy provided invaluable help with the field program; and the Cefas plankton team are thanked for analysing the numerous ichthyoplankton samples. The manuscript was greatly improved by discussions with Deidre Brophy and the comments of 3 anonymous reviewers.

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Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway

*Submitted: December 4, 2006; Accepted: March 13, 2007
Proofs received from author(s): August 15, 2007*