



Spatial and temporal variability in larval connectivity of North Sea plaice *Pleuronectes platessa* between spawning grounds and coastal European nurseries

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ABSTRACT: Annual year-class strength in North Sea plaice *Pleuronectes platessa* Linnaeus, 1758 appears to be determined by the connectivity of eggs and larvae between open-sea spawning grounds and coastal nursery areas. Hydrodynamic modelling studies indicate that coastal nurseries can be supplied with larvae from multiple offshore spawning locations. To verify this, we compared relative size-frequency distributions of demersal juvenile plaice just after larval immigration between coastal nurseries as a proxy for larval origin. During 12 yr, up to 21 stations in the Dutch coastal zone and international Wadden Sea were visited and sampled at the beginning of May at the end of larval immigration. The results of the size-frequency analysis showed 2 distinct clusters of stations. The first cluster included all stations along the Dutch coast and Wadden Sea up to Wangerooge in the German East Frisian Wadden Sea, most likely dominated by supply from spawning grounds in the Southern Bight, with contributions from the English Channel and the Dogger Bank. The second cluster included all stations in the North Frisian Wadden Sea, most likely supplied from spawning grounds in the German Bight and near the Dogger Bank. The higher interannual variability in the first cluster might be caused by a larger variability in the relative contributions from multiple spawning areas (English Channel, Southern Bight, Dogger Bank). The comparison of the relative size-frequency distributions at the end of larval immigration introduced in this study may also be a useful tool for the validation of connectivity modelling studies in other areas and for other species.

KEY WORDS: Wadden Sea · North Sea · Coastal nursery · Flatfish · Plaice · Larval supply · Larval connectivity · Spatial variability · Temporal variability

1. INTRODUCTION

In many fish species, the life cycle consists of a sequence of an egg, larval, juvenile and adult stage. Already more than a century ago, Hjort (1914, 1926) proposed the hypothesis that the strength of a year-class is annually controlled during a critical phase in early life history when the numbers of individuals are at a maximum. Presently, the general consensus is

that year-class strength in marine fishes is primarily determined during the early life history (Leggett & DeBlois 1994, van der Veer et al. 2000, Beggs & Nash 2007, Taylor et al. 2010). In many species, the early life stages include a pelagic phase with passive drift and/or active transport of eggs and developing larvae from spawning grounds towards juvenile habitats (e.g. see Secor 2015). Therefore, studies on year-class strength have focused on the connectivity and dis-

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persal between the egg, larval and juvenile habitats.

One of the species studied in much detail over the years is the flatfish species plaice *Pleuronectes platessa* Linnaeus, 1758. The life cycle of plaice and other flatfishes is biphasic and includes a dispersive pelagic and a more sedentary demersal phase. In the North Sea, spawning of plaice is widespread, with high concentrations in a number of well-defined areas, such as the Southern Bight, Dogger Bank, Flamborough Head and German Bight (for an overview, see Taylor et al. 2007). At the end of the pelagic larval stage, the larvae metamorphose and settle and concentrate in shallow coastal areas, so-called nursery areas, along the British and European coast, where they spend their juvenile life stage (for an overview, see Gibson 1999). The clear link between spawning grounds and nursery areas in the North Sea makes plaice an ideal species for studying connectivity and dispersal between the egg, larval and juvenile habitats in a strong hydrodynamic environment.

The first connectivity studies on plaice were extensive field surveys on the Southern Bight spawning grounds in the southern North Sea, and they supported the hypothesis of Hjort (1914, 1926) that year-class fluctuations in plaice are generated as early as during the egg stage (Harding et al. 1978, Brander & Houghton 1982). These multi-year pelagic plaice egg and larval field studies also showed an inverse relationship between year-class strength and water temperature in the spawning area in the southern North Sea and English Channel (Harding et al. 1978). Such field surveys are labour- and cost-intensive, and with the development of small beam trawls (for an overview, see Kuipers et al. 1992), it became popular to obtain information on connectivity by means of demersal studies on immigrating and just-settling juvenile plaice. These studies found significant inverse relationships similar to the open-sea field surveys. At the Balgzand intertidal nursery area in the western Dutch Wadden Sea, the annual index of abundance of newly settled plaice was inversely correlated with the February temperature of that year at the spawning grounds in the Southern Bight of the North Sea (van der Veer 1986, van der Veer & Witte 1999). An inverse relationship between abundance of settled plaice and water temperature during the early life stages was also found at a large spatial scale for various subpopulations of plaice around the UK (Fox et al. 2000).

Multiple factors may be responsible for the inverse relationship of year-class strength with seawater temperature during early life. Temperature changes both the development rate and egg mortality (Bannister et

al. 1974, Harding et al. 1978, van der Land 1991), and also affects metabolic costs and predation pressure (Zijlstra & Witte 1985). Water temperature in winter is typically a reflection of the general weather system in the southern North Sea: average conditions consist of southwesterly winds with relatively mild temperatures and anti-clockwise residual currents, whereas low temperatures are often connected with easterly winds, driving an atypical clockwise water circulation pattern (Otto et al. 1990) that affects the egg and larval drift (van der Veer & Witte 1999). Due to the presence of various spawning concentrations of plaice in the North Sea, differences in hydrodynamic circulation can also result in differences in mixing of eggs and larvae from various spawning grounds during drift. The relative importance of these multiple factors is impossible to disentangle in field studies.

With the development of sophisticated hydrodynamic circulation models coupled with particle tracking, a new tool for studying connectivity and dispersal under realistic climatic forcing and temperature conditions became available. The first modelling studies focused on the interannual variability in drift of plaice eggs and larvae from a single spawning area in the Southern Bight of the North Sea towards Dutch coastal nursery areas. With a general 2D hydrodynamic circulation model with realistic tidal and meteorological wind forcing, particle tracking indicated that interannual variability in transport was large and of the same order of magnitude as observed year-to-year variations in larval immigration patterns into the western Wadden Sea (van der Veer et al. 1998). More detailed studies with a 3D hydrodynamic circulation model also concluded that meteorologically driven variability in the hydrodynamics of the southern North Sea greatly affects plaice egg and larval drift patterns (Bolle et al. 2009), while behavioural components such as selective tidal transport (Talbot 1977, Rijnsdorp et al. 1985) also play a role (de Graaf et al. 2004, Bolle et al. 2009). A broader study including multiple plaice spawning grounds in the North Sea, with temperature-dependent development and stage-specific behaviour of eggs and larvae, also stressed the importance of not only variability in hydrodynamic circulation but also water temperature (Hufnagl et al. 2013). The modelling studies also suggested that eggs and larvae from various spawning grounds could get mixed during drift (Hufnagl et al. 2013, Tiessen et al. 2014, Barbut et al. 2019).

The biophysical model studies suggest that larval plaice migrating into coastal nurseries might originate from various spawning grounds; however, these findings require validation. Potential validation tools

are otolith microchemistry and otolith daily increment analysis. Otolith microchemistry has been used successfully to distinguish between juvenile and adult habitats for mobile species (Gillanders et al. 2003) including sole (Cuveliers et al. 2010, Delerue-Ricard et al. 2019). It has also been applied to the larval phase, but only for species with distinct freshwater and marine life phases (Warburton et al. 2018). In juvenile sole, otolith multi-elemental signatures of the larval phase point toward an extensive connectivity of individuals originating from different spawning grounds (Delerue-Ricard et al. 2019). For plaice, environmental gradients in the North Sea may also be strong enough to distinguish between spawning grounds by means of otolith multi-elemental signatures. A first study of daily otolith increment analyses for larval plaice immigrating into the western Wadden Sea at one location demonstrated differences in larval age and immigration with a suggestion of contributions from multiple spawning grounds (Hovenkamp 1991). Otolith microchemistry of larval plaice has not been studied thus far.

In this paper, we focus on a large scale with an alternative approach: the size-frequency distribution of juvenile plaice at the end of larval immigration for the analysis of the connectivity between spawning grounds and nurseries. Size is considered as a proxy for the timing of immigrating and settling larvae, based on the linear relationship between fish size and the number of days after settlement (Cardoso et al. 2016). We first confirmed the hypothesis that size-frequency distributions of settled plaice at the end of larval immigration are an indicator of annual plaice larval immigration patterns using independent historic data from the Balgzand plaice nursery area (van der Veer 1986). Over 3 yr (1980–1982), both larval immigration and demersal juvenile plaice were followed weekly and biweekly, respectively. Larval immigration patterns differed among years and resulted in significant differences in size-frequency distributions (see the Appendix). Consequently, (1) the size-frequency distribution of just-settled plaice at the end of larval immigration is a reflection of the timing and pattern in larval immigration, and (2) differences in size-frequency distribution between locations are a reflection of differences in contribution from the various spawning grounds. Correspondence in size-frequency distribution between adjacent locations would represent a common larval immigration pattern and hence origin.

In this study, the spatial and temporal variability in larval connectivity of North Sea plaice between

spawning grounds and coastal European nurseries was determined by sampling and analysing up to 21 nursery areas along the Dutch, German and Danish coasts at the end of larval plaice immigration in spring during a 12 yr period (1999–2010).

2. MATERIALS AND METHODS

Spawning of plaice occurs all over the North Sea, with higher concentrations in different areas like the English Channel, Southern Bight, a Transition Area south of the Dogger Bank, the Borkum area in the German Bight and Flamborough Head (Fig. 1A). The Dutch coast and the international Wadden Sea mainly consist of soft sandy sediments, and these areas are important nursery grounds for plaice (Zijlstra 1972, van Beek et al. 1989).

2.1. Sampling

Sampling started in 1999 and continued until 2010 (Table 1, Fig. 1B). In 1999, sampling was restricted to the Dutch Wadden Sea. In 2000, sampling was expanded to some stations in the German and Danish Wadden Sea, and from 2001 onwards, 14 locations covering the whole Wadden Sea area were used. In addition, the Dutch coast was sampled during 2005–2009. In 2005, Stn 17 (Neuwerk) was skipped due to bad weather conditions. For coding and locations of the stations, see Table 2.

Sampling occurred during a restricted time window at the beginning of May, since at that time, larval immigration ends and year-class strength is determined (van der Veer 1986). At each sampling station, typically 200 0-group plaice were collected at a water depth of less than 1 m, irrespective of tidal phase. In water depths over 0.5 m, sampling was done with a 1.9 m beam trawl (1 tickler chain, net mesh size 5 × 5 mm) towed by a rubber dinghy with a 25 HP outboard engine at a speed of approximately 35 m min⁻¹ (Riley & Corlett 1966). In water depths less than 0.5 m, samples were taken using a 1 m beam trawl (1 tickler chain, net mesh size 5 × 5 mm) towed by hand. In addition, water temperature and salinity were recorded with standard equipment. The locations of the hauls were established using a global positioning system, and the length of the hauls was assessed with a metre wheel fitted to the trawl.

Catches were immediately sorted out alive, and 0-group plaice were preserved in 70% ethanol.

Table 1. Period of sampling and stations sampled in the various years. For coding, see Fig. 1B and Table 2

Cruise	Dutch coast	Wadden Sea	Stations sampled
1999	—	3–8 May	8–13
2000	—	10–14 May	8–15
2001	—	1–7 May	8–21
2002	—	30 April–10 May	8–21
2003	—	6–12 May	8–21
2004	—	6–14 May	8–21
2005	25–27 April	3–10 May	1–21 (except 17)
2006	24–27 April	1–8 May	1–21
2007	30 April–3 May	7–14 May	1–21
2008	22–24 April	5–13 May	1–21
2009	27–29 April	30 April–10 May	1–21
2010	—	8–19 May	8–21

Length was measured to the nearest 1 mm total length after 24 h without correction for shrinkage. Subsequently, samples were stored in 70% ethanol at 4°C.

2.2. Data handling

For each station, the size-distribution was moved forwards or backwards to a common date (7 May) to allow the direct comparison of the various stations and years. First, for each haul, numbers caught were corrected for size-selective mesh and catch efficiency after Kuipers (1975) and Dapper (1978). Next, for each year, the size-frequency distribution of each sampling station was standardised to the date of 7 May, according to the following procedure: first, for each sampling station, the difference in number of days between actual sampling and 7 May of that year was determined. Subsequently, the observed size-frequency distribution was corrected to 7 May by assuming a maximum growth (G ; mm):

$$G = dL \cdot D \quad (\text{mm}) \quad (1)$$

where D is the time difference in days between the sampling date and 7 May, and dL is the temperature-dependent length growth rate (mm d^{-1}), which was determined according to the growth model under excess of food for small 0-group plaice (Glazenburg 1983):

$$dL = (1.3 \cdot T + 1.7)/30 \quad (\text{mm d}^{-1}) \quad (2)$$

where T represents the water temperature ($^{\circ}\text{C}$).

The size-frequency distribution was moved forwards or backwards with the integer of $G + 0.5$ (mm). Since sampling was restricted to a short period of

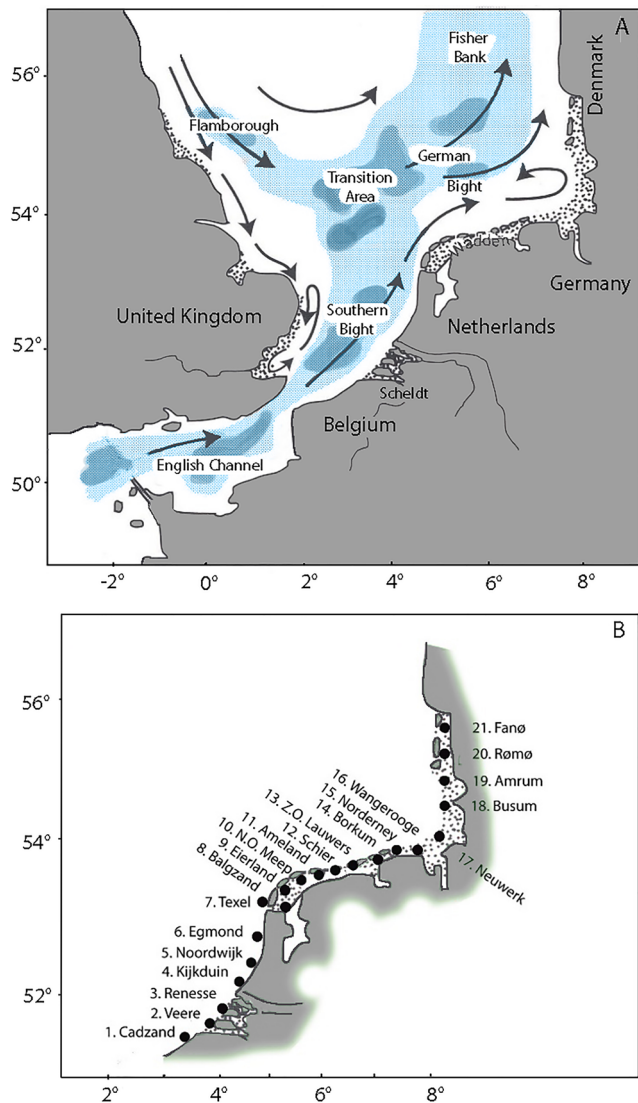


Fig. 1. (A) Spawning areas (blue; dark blue indicates main areas of concentration) and main nursery areas (grey dots) of North Sea plaice, based on historical and recent information. For more information, see Aurich (1941), Simpson (1959) and Taylor et al. (2007). Arrows indicate residual currents. (B) Sampling stations along the European North Sea coast from the south of the Netherlands to Denmark. Grey dots refer to Wadden Sea nursery areas

time, most size-frequency distributions were corrected (moved) by less than 3 mm. Next, due to differences in the number of individuals caught per station, all size-frequency distributions were normalised into relative size-frequency distributions. Finally, for each station and for each year, all relative size-frequency distributions were converted into cumulative relative size-frequency distributions (CRSFDs) ranging from 0 to 1.

Table 2. Coding and location of the various sampling stations along the Dutch coast and in the Wadden Sea

Station	Station name	Code	Location	Latitude	Longitude
1	Cadzand	CADZ	Dutch coast	51° 23.018"	3° 27.582"
2	Veere	VEER	Dutch coast	51° 35.308"	3° 23.869"
3	Renesse	RENE	Dutch coast	51° 44.523"	3° 48.564"
4	Kijkduin	KIJK	Dutch coast	52° 04.234"	4° 13.206"
5	Noordwijk	NOOR	Dutch coast	52° 14.795"	4° 25.905"
6	Egmond	EGMO	Dutch coast	52° 37.351"	4° 37.164"
7	Texel	TEXE	Dutch coast	53° 02.331"	4° 42.705"
8	Balgzand	BALG	Dutch Wadden Sea	52° 57.736"	4° 55.550"
9	Eierland	EIER	Dutch Wadden Sea	53° 13.207"	4° 57.150"
10	N.O.Meep	NOME	Dutch Wadden Sea	53° 18.977"	5° 26.027"
11	Ameland	AMEL	Dutch Wadden Sea	53° 25.624"	5° 47.468"
12	Schiermonnikoog	SCHI	Dutch Wadden Sea	53° 26.610"	6° 10.409"
13	Z.O.Lauwers	ZOLA	Dutch Wadden Sea	53° 29.209"	6° 28.870"
14	Borkum	BORK	German East Frisian Wadden Sea	53° 35.779"	6° 48.572"
15	Norderney	NORD	German East Frisian Wadden Sea	53° 41.694"	7° 14.861"
16	Wangerooge	WANG	German East Frisian Wadden Sea	53° 46.446"	7° 57.894"
17	Neuwerk	NEUW	Elbe estuary German Wadden Sea	53° 54.749"	8° 23.136"
18	Büsum	BUSU	German North Frisian Wadden Sea	54° 09.111"	8° 43.837"
19	Amrum	AMRU	German North Frisian Wadden Sea	54° 37.441"	8° 23.924"
20	Rømø	ROMO	Danish Wadden Sea	55° 03.608"	8° 31.426"
21	Fanø	FANO	Danish Wadden Sea	55° 18.588"	8° 27.146"

2.3. Data analysis

An analysis of the spatial variability and an analysis of the temporal (interannual) variability in the CRSFDs among all stations was performed. The analysis of the spatial variability among the stations was restricted to the years with data for all stations (2005–2009). For these years, the CRSFDs of the individual years were averaged per station. The analysis of the temporal (interannual) variability between stations was based on the CRSFD for each year of sampling.

Both analyses focused on the maximum difference between the CRSFDs, which was determined as follows: for all possible combinations of 2 stations, the 2 CRSFDs were compared, and for each mm size class, the difference was calculated. Next, the maximum difference (largest value) in CRSFD was selected from the resulting distribution. The maximum difference between the 2 CRSFDs was used to apply the Kolmogorov-Smirnov goodness-of-fit test for detecting significant differences between size-frequency distributions: 2 size frequencies are significantly different when the maximum difference in the CRSFDs exceeds 0.192 at a critical value of 0.05, and 0.231 at a critical value of 0.01 (Chakravarti et al. 1967).

For each station, the maximum difference (largest value) in CRSFD with all other stations was compiled, and stations were tested for correspondence in their pattern of maximum difference by means of a Spear-

man rank correlation test. Next, correspondence in their pattern of maximum difference with the other stations was visualised by means of a principal component analysis (PCA).

All computations and analyses were done in R (R Core Team 2021). The graphics were made using the 'ggplot' package (Wickham 2009).

3. RESULTS

The along-coast patterns in mean length of 0-group plaice corrected to 7 May showed variability along the Dutch coast and in the western part of the Dutch Wadden Sea (Stns 1–7 and 8–11) and a slight decreasing tendency from around Ameland towards Fanø in Denmark (Stns 11–21) (Fig. 2). The pattern was visible in all years of sampling.

3.1. Spatial variability

Various combinations of stations showed significant differences between the mean CRSFDs for 2005–2009 (Table 3). It should be noted that for more critical levels of required significance, more stations will remain similar with the Kolmogorov-Smirnov goodness-of-fit test. Two clusters of stations with similar size distributions emerged: Stns 1–16 along the

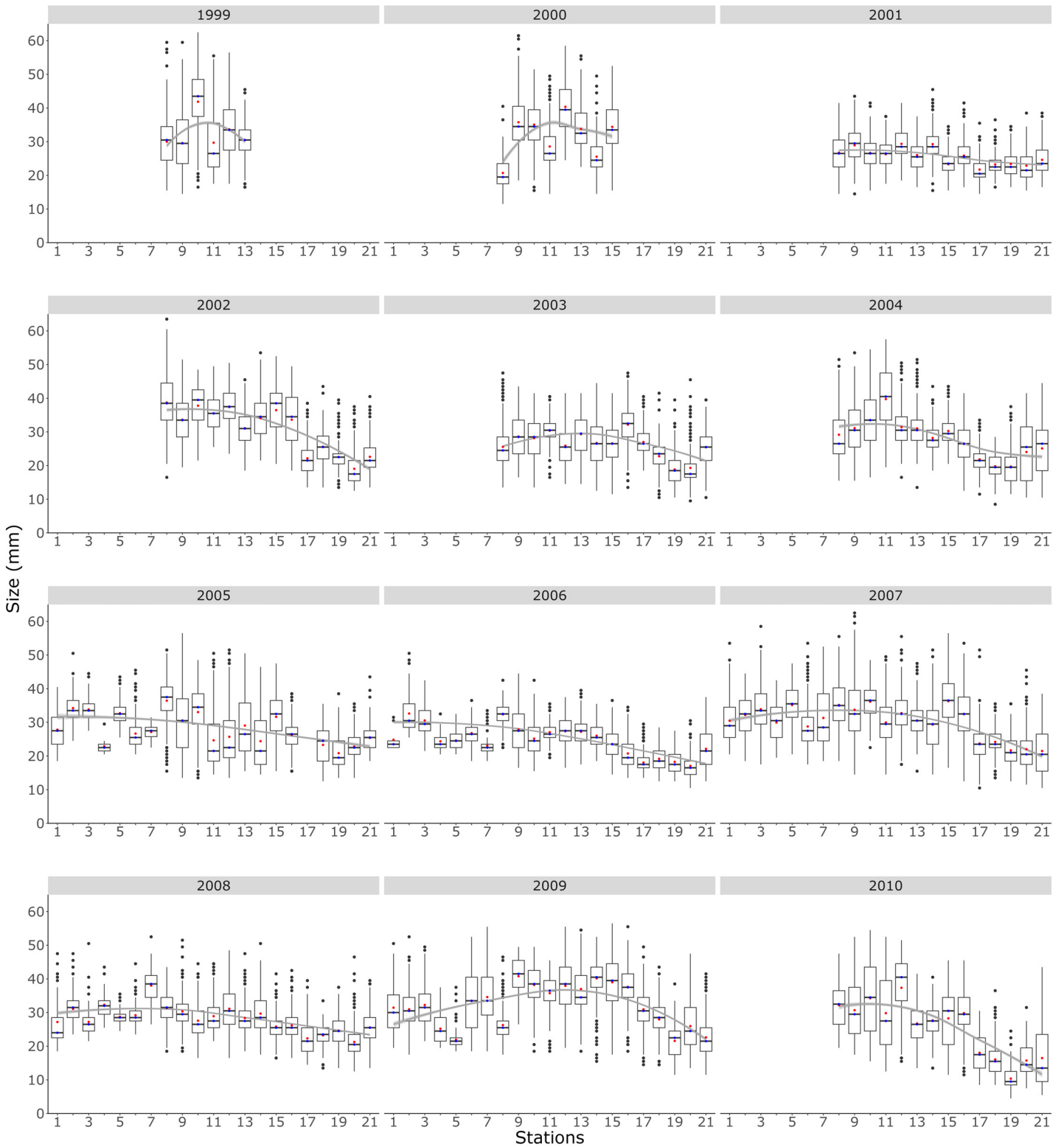


Fig. 2. Length of 0-group plaice, corrected to 7 May for all stations (for coding, see Table 2) and years along the European North Sea coast from the south of the Netherlands to Denmark. Horizontal blue thick line in each box is the median, red dot is the mean, the boxes define the hinge (25–75% quartile, and the line is 1.5 times the hinge). Points outside this interval are represented as dots. A local regression (LOESS) smoother (grey line) is added

Table 3. Maximum difference between the mean cumulative relative size-frequency distribution (2005–2009) of the various stations. Green: not significantly different (at $p < 0.01$). For locations of stations and codes, see Fig. 1 and Table 2

Station	Wadden Sea																				
	Dutch coast										Wadden Sea										
	Dutch Wadden Sea					East Frisian Wadden Sea					Elbe	North Frisian Wadden Sea									
CODE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	CADZ	VEER	RENE	KJK	NOOR	EGMO	TEXE	BALG	EIER	NOME	AMEL	SCHI	ZOLA	BORK	NORD	WANG	NEUW	BUSU	AMRU	ROMO	FANO
1	CADZ	0.393	0.332	0.127	0.133	0.179	0.161	0.325	0.266	0.276	0.173	0.198	0.226	0.136	0.205	0.138	0.385	0.284	0.486	0.521	0.334
2	VEER	0.393	0.103	0.434	0.293	0.340	0.254	0.077	0.143	0.154	0.267	0.197	0.205	0.266	0.235	0.334	0.572	0.620	0.731	0.708	0.595
3	RENE	0.332	0.103	0.374	0.221	0.249	0.186	0.103	0.148	0.140	0.171	0.156	0.107	0.196	0.177	0.259	0.514	0.531	0.666	0.660	0.505
4	KJK	0.127	0.434	0.374	0.221	0.175	0.206	0.369	0.311	0.319	0.214	0.237	0.267	0.188	0.259	0.146	0.320	0.225	0.408	0.410	0.272
5	NOOR	0.133	0.293	0.221	0.175	0.222	0.160	0.263	0.214	0.236	0.088	0.151	0.121	0.125	0.183	0.124	0.326	0.351	0.468	0.449	0.322
6	EGMO	0.179	0.340	0.249	0.222	0.139	0.155	0.340	0.279	0.299	0.104	0.209	0.157	0.148	0.219	0.163	0.411	0.340	0.513	0.549	0.359
7	TEXE	0.161	0.254	0.186	0.206	0.160	0.155	0.215	0.156	0.150	0.101	0.085	0.101	0.094	0.077	0.145	0.381	0.379	0.496	0.518	0.351
8	BALG	0.325	0.077	0.103	0.369	0.263	0.340	0.215	0.095	0.083	0.240	0.136	0.184	0.215	0.162	0.275	0.498	0.569	0.658	0.631	0.546
9	EIER	0.266	0.143	0.148	0.311	0.214	0.156	0.095	0.156	0.073	0.182	0.078	0.162	0.156	0.108	0.218	0.444	0.510	0.603	0.565	0.487
10	NOME	0.276	0.154	0.140	0.319	0.236	0.150	0.083	0.073	0.195	0.195	0.092	0.183	0.163	0.092	0.207	0.428	0.501	0.576	0.555	0.484
11	AMEL	0.173	0.267	0.171	0.214	0.088	0.104	0.240	0.182	0.195	0.105	0.105	0.068	0.066	0.131	0.113	0.378	0.372	0.507	0.525	0.345
12	SCHI	0.198	0.197	0.156	0.237	0.151	0.209	0.136	0.078	0.092	0.105	0.099	0.099	0.084	0.043	0.152	0.377	0.440	0.539	0.515	0.421
13	ZOLA	0.226	0.205	0.107	0.267	0.121	0.157	0.184	0.162	0.183	0.068	0.099	0.090	0.090	0.129	0.153	0.406	0.428	0.560	0.553	0.399
14	BORK	0.136	0.266	0.196	0.188	0.125	0.094	0.215	0.156	0.163	0.066	0.084	0.090	0.090	0.083	0.069	0.323	0.358	0.470	0.469	0.338
15	NORD	0.205	0.235	0.177	0.259	0.183	0.219	0.162	0.108	0.092	0.131	0.043	0.129	0.083	0.121	0.121	0.348	0.414	0.497	0.495	0.399
16	WANG	0.138	0.334	0.259	0.146	0.124	0.145	0.275	0.218	0.207	0.113	0.152	0.153	0.069	0.121	0.121	0.266	0.293	0.411	0.412	0.280
17	NEUW	0.385	0.572	0.514	0.320	0.326	0.411	0.498	0.444	0.428	0.378	0.377	0.406	0.323	0.348	0.266	0.266	0.104	0.168	0.147	0.073
18	BUSU	0.284	0.620	0.531	0.225	0.351	0.379	0.569	0.510	0.501	0.372	0.440	0.428	0.358	0.414	0.293	0.104	0.203	0.237	0.053	0.053
19	AMRU	0.486	0.731	0.666	0.408	0.468	0.513	0.658	0.603	0.576	0.507	0.539	0.560	0.470	0.497	0.411	0.168	0.203	0.051	0.174	0.174
20	ROMO	0.521	0.708	0.660	0.410	0.449	0.518	0.631	0.565	0.555	0.525	0.515	0.553	0.469	0.495	0.412	0.147	0.237	0.051	0.191	0.191
21	FANO	0.334	0.595	0.505	0.272	0.322	0.359	0.546	0.487	0.484	0.345	0.421	0.399	0.338	0.399	0.280	0.073	0.053	0.174	0.191	0.191

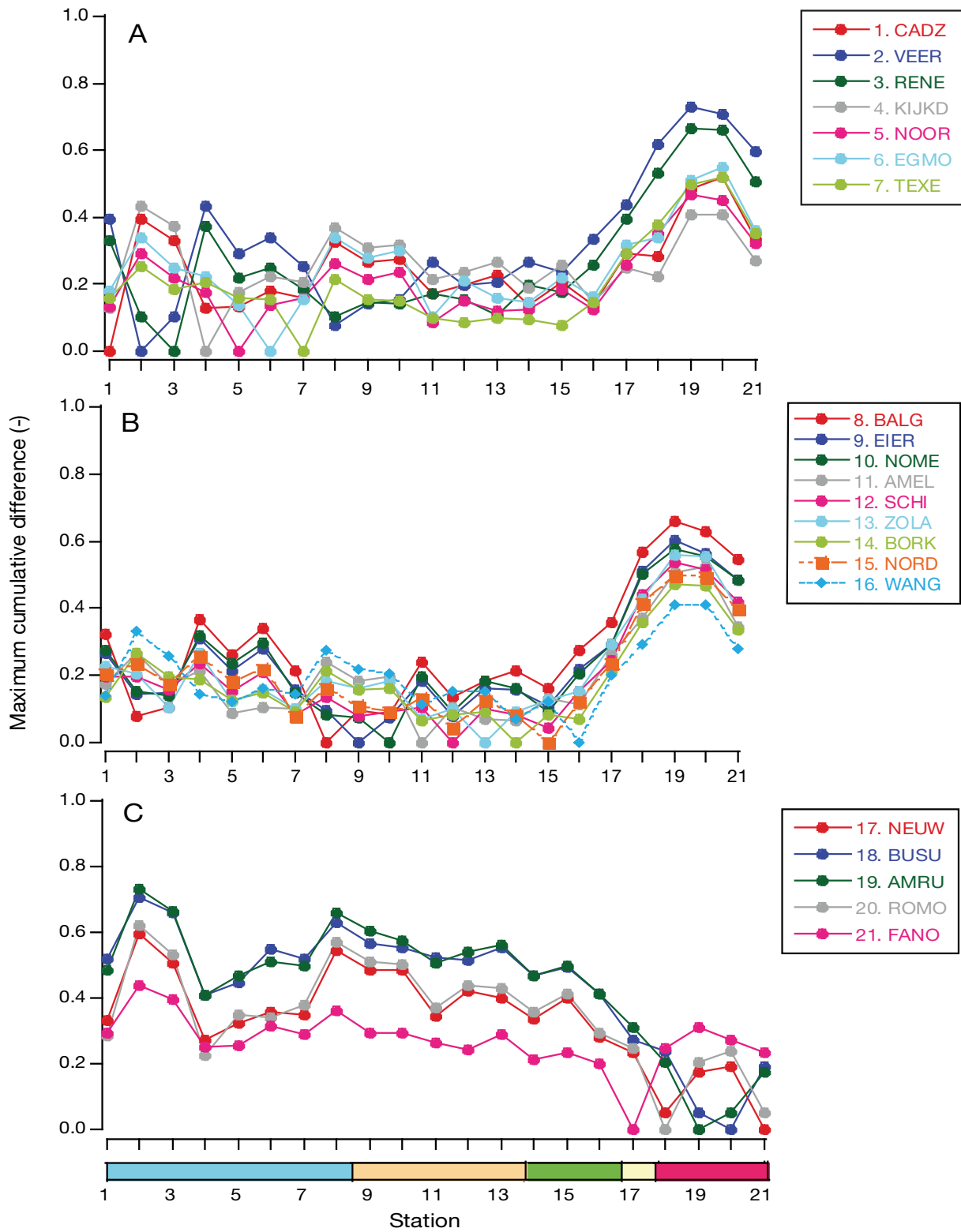


Fig. 3. Maximum difference between the mean cumulative relative size-frequency distribution (2005–2009) of a given station and all other stations. (A) Stations along the Dutch coast, (B) stations in the Dutch and North Frisian Wadden Sea, (C) stations in the East Frisian Wadden Sea. The bar at the bottom refers to Dutch coastal stations (1–8), Dutch Wadden Sea stations (9–13), East Frisian Wadden Sea stations (15–16), Elbe (17) and North Frisian Wadden Sea stations (18–21)

Dutch coast, Dutch Wadden Sea and East Frisian Wadden Sea and Stns 17–21 in the Elbe and the North Frisian Wadden Sea (Table 3).

The correspondence in the pattern of maximum difference in mean CRSFDs (2005–2009) with the other stations was irregular for the stations along the Dutch coast (Stns 1–7), with many of the combinations not being similar (Fig. 3; for Spearman rank correlations, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m733p111_supp.pdf). Most of the Dutch and East Frisian Wadden Sea stations (Stns 8–16) were not significantly different from each other ($p > 0.01$), but were significantly different from the North Frisian stations (Stns 17–21). The North Frisian stations were not significantly different from each other ($p > 0.01$), but were significantly different from all other stations.

A PCA plot of the stations with respect to the correspondence in pattern of a station in maximum difference in the mean CRSFDs for 2005–2009 with the other stations showed a separation by the first principal component into 2 clusters: the North Frisian Stns 17–21 (Neuwerk – Fanø) and all other stations (Stns 1–16) without a separation between the stations along the Dutch coast and in the Dutch and East Frisian Wadden Sea (Fig. 4). The cluster of Stns 1–16

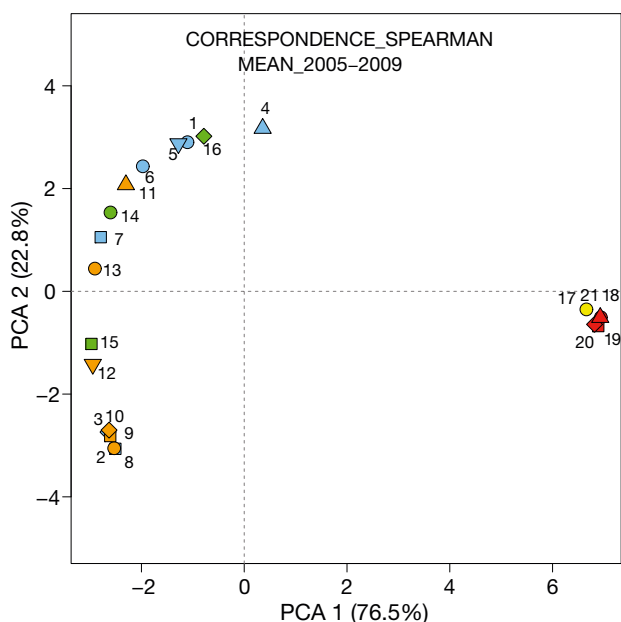


Fig. 4. Principal component analysis (PCA) plot of the stations with respect to their correspondence in pattern in maximum difference in the mean cumulative relative size-frequency distribution (2005–2009) with the other stations (for data, see Table S1 in the Supplement). Blue: Dutch coastal stations; light orange: Dutch Wadden Sea stations; green: East Frisian Wadden Sea stations; yellow Elbe; red: North Frisian Wadden Sea stations. Coding: see Fig. 1 and Table 2

showed differences along the second principal component, without a clear pattern between coastal (Stns 1–7) and Wadden Sea (Stns 8–16) stations.

3.2. Temporal variability

In all years, stations along the Dutch coast and Wadden Sea (Stns 1–16) were almost always different from those in the North Frisian Wadden Sea (Stns 17–21). The stations with similar size distributions varied over the years, yet a clear pattern was apparent (Table S2). In 8 out of 10 years, 2 clusters of stations (Stns 1–16 and 17–21) with similar patterns could be distinguished. In 2005 and 2009, the clusters showed some overlap. In all years, the North Frisian Wadden Sea stations showed a significantly similar pattern, except for 1 station (Stn 17) in 2009. Also in 2010, all Wadden Sea stations of cluster 1 (Stns 8–16) were significantly correlated. In the other years, there was variability, with no clear pattern (Table S2).

The average spatial pattern for the years 2005–2009 was reflected in the PCA for all individual years (Fig. 5; Tables S3 & S4), albeit with interannual variability. In all years in which the North Frisian Stns 17–21 were sampled (2001–2010), they clustered together. The other stations along the Dutch coast (Stns 1–7) and in the Dutch and German Wadden Sea (Stns 8–16) formed another cluster in most years, separated from the North Frisian Stns 17–21. In 2009, 2 stations along the Dutch coast (Stns 4 and 5) overlapped with the North Frisian stations. In most years, except 2005, most variability was found along the second PCA axis. Variability between the stations along the Dutch coast, in the Dutch Wadden Sea and in the German Wadden Sea was large in 2005, 2006, 2008 and 2009, when stations overlapped without a clear pattern. In 2001, 2002, 2003, 2007 and 2010, variability between stations was small, with a suggestion of 2 smaller subclusters.

4. DISCUSSION

The results of this study show that the size-frequency distributions of just-settled plaice at the end of larval immigration can be used for analyses of spatial and temporal variability in larval immigration patterns between nursery areas. This proxy can only be applied if there is large enough spatial and temporal variability in larval immigration and hence size-frequency distributions. In this respect, North Sea plaice is an ideal study species for a number of rea-

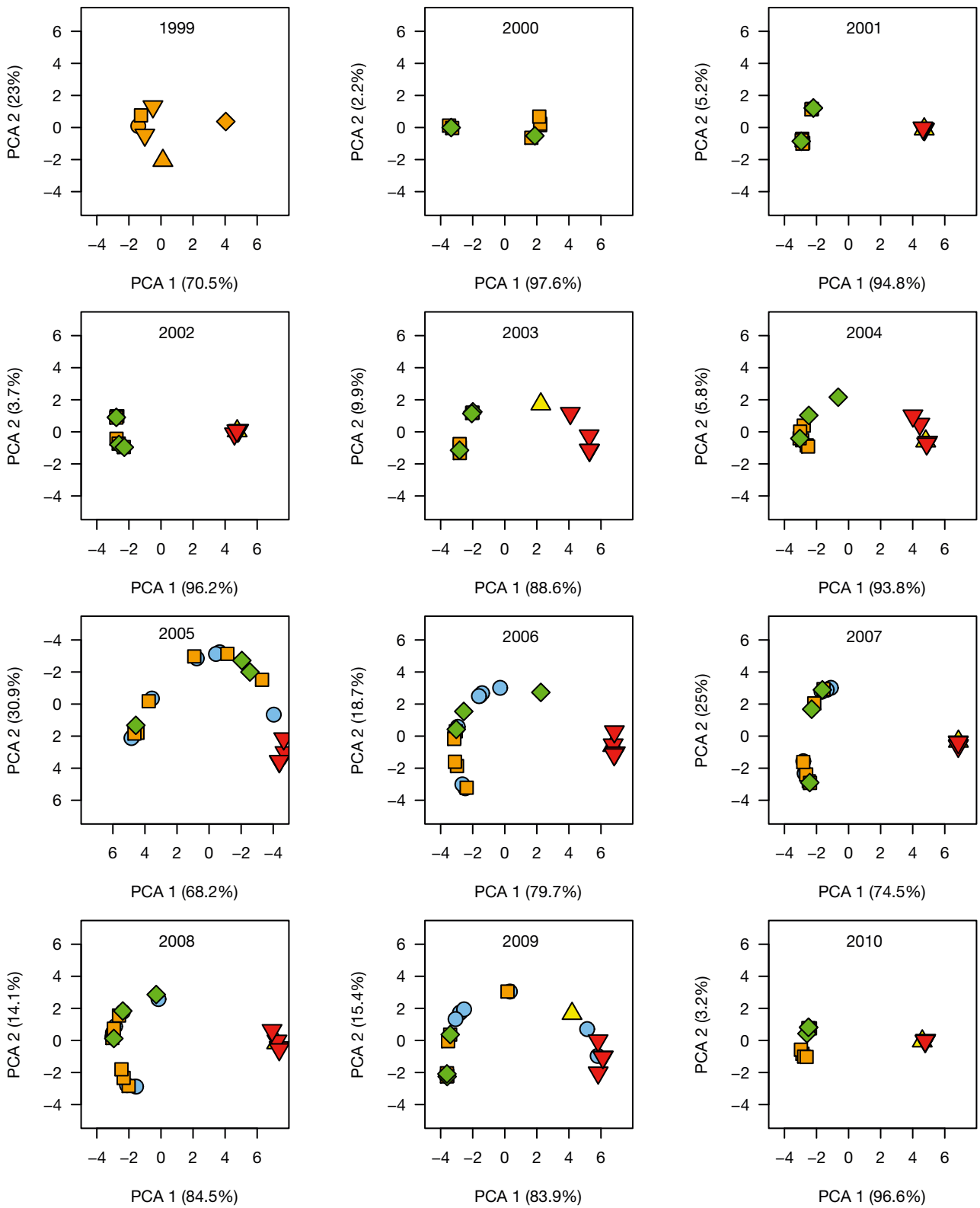


Fig. 5. PCA plot of the stations with respect to their correspondence in pattern in maximum difference in the mean cumulative relative size-frequency distribution with the other stations for the years 1999 to 2000 (for data, see Table S3). For symbol colours, see Fig. 4

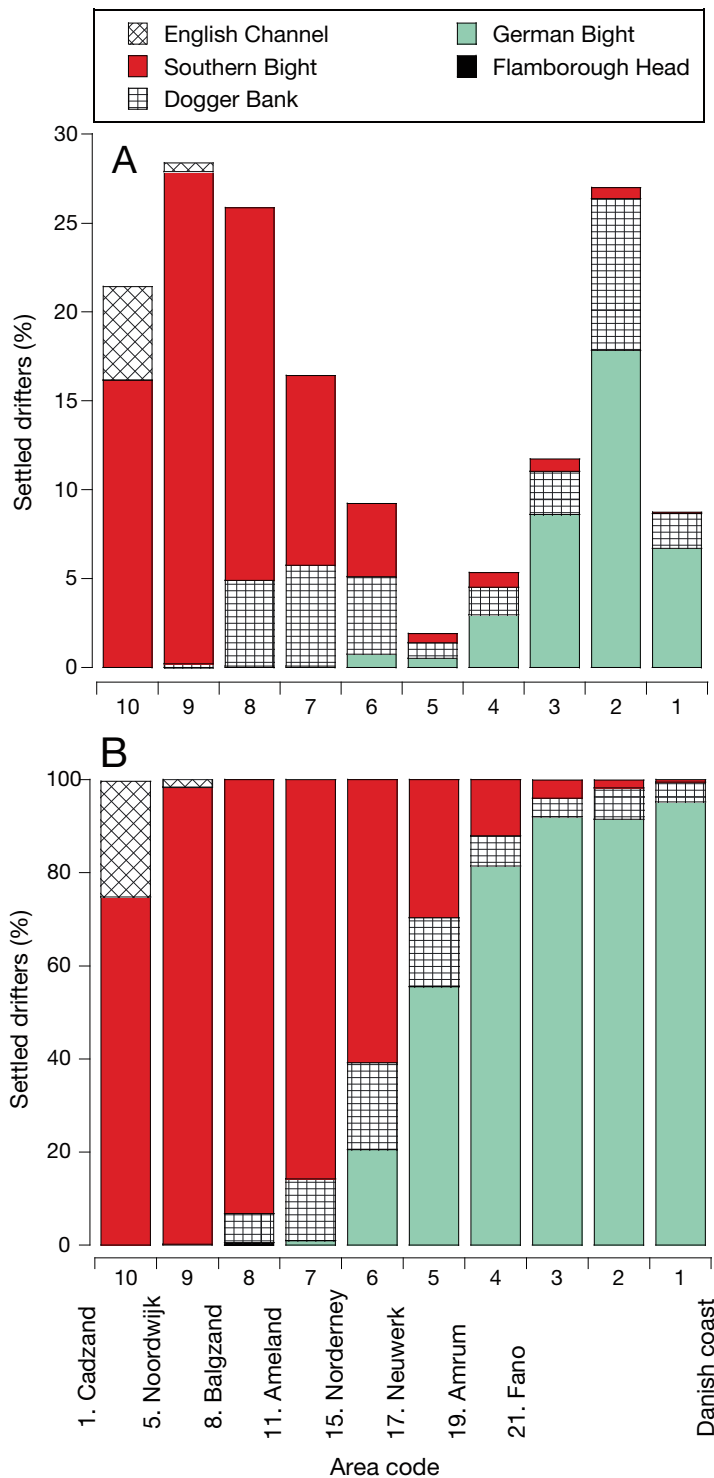


Fig. 6. Model study of the distribution of successfully settled drifters originating from various plaice spawning areas over the nursery area between Cadzand and the north of Denmark after Hufnagl et al. (2013). Area code 1–10 after Hufnagl et al. (2013). Corresponding stations in this study are added vertically. (A) Distribution of successfully settled drifters (%) from various spawning areas. (B) Origin of successfully settled drifters (%) in the various nursery zones

sons. First of all, there is large spatial variability in spawning areas in the North Sea, with spawning being widespread, with high concentrations in a number of well-defined areas such as the English Channel, Southern Bight, south of the Dogger Bank, the Borkum area of the German Bight and Flamborough Head (Aurich 1941, Wimpenny 1953, de Veen 1978, van der Land 1991, Taylor et al. 2007, Ellis et al. 2012). There is also a difference in time of the start of spawning, varying and depending upon latitude, from December in the south to May and June in the far north (Aurich 1941, Wimpenny 1953), and the period of spawning is a few months (Aurich 1941, Wimpenny 1953). Furthermore, spatial and temporal variability in water temperature conditions between different spawning grounds in the North Sea causes fluctuations in the development of eggs and larvae (Ryland & Nichols 1975), resulting in differences in larval drift duration. Finally, spatial and temporal variability in meteorological conditions causes variation in hydrodynamic circulation in the North Sea and variation in potential mixing of patches of developing eggs and larvae originating from different spawning grounds (Hufnagl et al. 2013, Tiessen et al. 2014).

This means that spatial and temporal variability in larval immigration might be expected in all nursery areas and has indeed been found in all larval immigration field studies such as in the Dutch Delta area (Rijnsdorp et al. 1985) and the western Dutch Wadden Sea (Creutzberg et al. 1978, Rijnsdorp et al. 1985, van der Veer 1986, Hovenkamp 1991). Crucial for the application of the size distribution at the end of larval immigration as a proxy for characterising larval immigration patterns is that larval settlement does not immediately occur when larvae first reach their coastal nurseries, but only when they have completed development, such as in plaice (Ryland 1966, Creutzberg et al. 1978): larvae always settle within a fixed size range between 10 and 15 mm (Macer 1967, Edwards & Steele 1968, Lockwood 1974, Creutzberg et al. 1978, Rijnsdorp et al. 1985, van der Veer 1986).

In applying this proxy, size- and density-dependent mortality operating during and shortly after settlement (van der Veer 1986, van der Veer et al. 1997) might potentially cause some bias. However, in the Dutch

Wadden Sea, size- and density-dependent mortality was weak compared to the overall mortality and did not affect the characterisation of the larval immigration pattern (van der Veer & Bergman 1987; also see the Appendix), but this might be different in other areas. Furthermore, sampling during a relatively short period of time (as in this study) might not be optimal for all locations sampled. In this study, we tried to reduce potential bias in sampling as much as possible by restricting sampling to the Dutch coast and international Wadden Sea only. In some years, some still-settling larvae were found during sampling, but numbers were always low. Extending the spatial scale of sampling would most likely not be possible with the present sampling scheme and would also require sampling later in May or even in June.

The size-frequency distributions of just-settled individuals at the end of their larval immigration and settlement might also be a tool for studying the connectivity patterns in other North Sea flatfish species (flounder, dab, sole, turbot and brill), each with its own species-specific larval traits (Barbut et al. 2019), and also for other flatfish species with a similar life cycle (see Duffy-Anderson et al. 2015).

4.1. Spatial variability in larval supply

Connectivity and dispersal between the egg, larval and juvenile habitats is the outcome of complex biophysical interactions of temperature-dependent and interacting processes (such as development and metabolic rate, egg and larval mortality) in combination with developing larval behaviour operating at a large scale under different hydrodynamic conditions and forcing. This makes the study of population connectivity immensely difficult, and with the rapidly increasing computational capacity over the last decades, most estimates are based on the predictions from more and more complicated and detailed biophysical models (for review, see Duffy-Anderson et al. 2015, Swearer et al. 2019). Swearer et al. (2019) stressed the need not only for greater emphasis on validation of the underlying model assumptions, but also for verifying and testing model predictions with empirically derived data. Also, for North Sea plaice, the most recent connectivity studies are based on unverified predictions of hydrodynamic modelling studies.

For North Sea plaice, the general opinion has always been that in the North Sea where residual currents are strong (Otto et al. 1990), the main plaice

spawning grounds are a reflection of the nursery grounds, whereby spawning grounds are located upstream of the nursery grounds (Gibson 1999). Implicitly, this also suggests a strong connectivity between various spawning grounds and 'their' nursery grounds. As such, the Flamborough Head spawning ground would supply the east coast of the UK, the English Channel spawning ground the French and Belgian coastal nurseries, the Southern Bight spawning ground the Dutch Wadden Sea, the German Bight spawning ground the more northern nursery areas in the Wadden Sea and along the Danish coast, and the Dogger Bank spawning ground (or Transition Zone) would also be able to contribute to nursery areas along the European coast.

In fact, only few field studies have confirmed this general opinion by following the patches of developing eggs and larvae during drift from the spawning grounds towards the coastal nursery areas. Only the connectivity between the Southern Bight spawning area and coastal nursery grounds along the European coast and Dutch Wadden Sea has been demonstrated by extensive British surveys between 1947 and 1971 (for an overview, see Harding et al. 1978), and later by Hovenkamp (1990). Beverton & Lee (1965) analysed fluctuations in larval drift from the Southern Bight spawning grounds. In a normal winter (1962), larval drift occurred towards the Dutch coast and the Marsdiep inlet, whereas in a very cold winter (1963), larval drift was farther to the north, into the German Bight.

All further studies on connectivity of North Sea plaice in the open sea rely on predictions by hydrodynamic modelling studies. The first hydrodynamic circulation modelling studies focused on the Southern Bight spawning area and confirmed the potential links with the Dutch Wadden Sea (van der Veer et al. 1998, Bolle et al. 2009), and with the German Wadden Sea (de Graaf et al. 2004). Two broader studies included multiple plaice spawning grounds, and these suggest a link between English Channel spawning grounds and Belgian and Dutch coastal nurseries, and between the German Bight spawning ground and the Dutch and Danish Wadden Sea and Danish coastal nurseries (Hufnagl et al. 2013, Tiessen et al. 2014), thereby implying that eggs and larvae from various spawning grounds could get mixed during drift. Barbut et al. (2019) even stated that North Sea plaice represent a single mixed population, which is in line with the large spatial and temporal homogeneity found by microsatellite analysis (Hoarau et al. 2002).

Presently, the most detailed predictions about North Sea plaice larval connectivity were made by

Hufnagl et al. (2013), modelling a 31 yr period (1975–2006). Their main findings were that:

(1) There is larval connectivity between spawning grounds and nurseries along the Dutch coast and Wadden Sea, except for an area around the Elbe estuary with very low connectivity (Fig. 6A);

(2) The Southern Bight and the German Bight (and to a lesser extent the English Channel and the Dogger Bank) are the most important spawning areas supplying plaice larvae along the European coast (Fig. 6A);

(3) Along the Dutch coast and the East Frisian Wadden Sea, there was a cluster of stations with a dominant contribution from Southern Bight spawning grounds, whereas for stations along the North Frisian Wadden Sea, the main contribution originated from the German Bight spawning ground (Fig. 6B).

For the first time, we are able to test and validate part of the predictions of the modelling studies by Hufnagl et al. (2013) with the observation-based results of this study. In all years of sampling, juvenile plaice could be easily collected at all stations, indicating annual connectivity between spawning grounds and nurseries all along the Dutch coast and Wadden Sea, confirming and validating Hufnagl et al. (2013) (Finding 1 above). Only during and shortly after (within a year) shoreface nourishment activities along the Dutch coast, catches of juvenile plaice were very low (data not shown). This might be related to the preference of juvenile plaice for relatively fine sediments (Gibson & Robb 2000), similar to juvenile sole (Post et al. 2017). In our study, 2 clusters of stations could be identified: the stations along the Dutch coast from Cadzand up to Wangerooge and a separate cluster along the North Frisian stations (Neuwerk to Fanø), confirming and validating Hufnagl et al. (2013) (Finding 3). The 2 clusters of stations found in both the modelling study by Hufnagl et al. (2013) and in our study suggests that the Elbe estuary acts as a kind of a barrier, which may be related to the complicated hydrography of the area, with strong density gradients, dynamic and variable fronts, and many meanders and eddies (Becker et al. 1992). Folmer et al. (2014), studying the bivalve *Mytilus edulis*, also suggested that the water currents in the Ems and Elbe estuaries formed a barrier for larval transport. While we were successful in confirming Findings 1 and 3, we could not identify which spawning areas supply larvae to the coastal nursery areas along the European coast (Finding 2), although the variations in PC2 for the first cluster suggested variations in mixing of larvae originating from different spawning grounds (see also Section 4.2).

4.2. Temporal variability in larval supply

Field data show that temporal variability in larval supply to the nursery grounds can be substantial, both within a year and between years. Along the Dutch coast at the settling stage, larval densities could vary between almost zero and a few hundred individuals per 1000 m³ with different temporal patterns between neighbouring stations (Creutzberg et al. 1978, Rijnsdorp et al. 1985, van der Veer 1986). Among years, average densities could also vary by a factor of 10 (van der Veer 1986, Hovenkamp 1991). The various modelling studies also indicate large fluctuations in connectivity between plaice spawning grounds and nursery areas (van der Veer et al. 1998, Bolle et al. 2009, Hufnagl et al. 2013, Tiessen et al. 2014).

Despite these strong interannual fluctuations in larval supply, we found that the general overall pattern remained present in most of the years. The size-frequency distributions showed an overall decreasing mean size towards the more eastern and northern stations, though with some interannual variability. In some years, mean size was largest in the eastern Dutch Wadden Sea (Stns 11–13), with decreasing trends in both directions, suggesting earlier settlement in those directions.

In all years, the first 2 PCA axes explained more than 90% of the variability between stations. Not only in 2005–2009, but also in the other years, the separate clustering of the North Frisian stations (Stns 17–21) along the first PCA axis was visible, supporting that the first PCA axis is a reflection of the Elbe estuary acting as a kind of a barrier. In all individual years, all other stations clustered together, albeit with differences between years but without a clear pattern. For the second PCA axis, interannual variability in clustering was always lowest at the North Frisian stations (Stns 17–21). For the Dutch coast and the Dutch and East Frisian German Wadden Sea, variability between stations was in general substantial.

The cause of the higher interannual variation in the second PCA axis is unclear, but might reflect large temporal variability in the source of larval supply of the Dutch coast and the Dutch and East Frisian Wadden Sea (Rijnsdorp et al. 1985, van der Veer 1986). Interannual variability in the stations along the Dutch coast and Dutch and German East Frisian Wadden Sea was high, partly because these stations cover a larger range but also because larval supply can potentially originate from at least 3 spawning areas (English Channel, Southern Bight, Dogger Bank) (Hufnagl et al. 2013).

Insight in the underlying processes of the observed interannual variability is outside the scope of the present paper. The inverse relationship of year-class strength with seawater temperature during early life (van der Veer 1986, van der Veer & Witte 1999, Fox et al. 2000) points to water temperature either as a controlling factor with respect to development rate and egg mortality (Bannister et al. 1974, Harding et al. 1978, van der Land 1991), metabolic costs and predation pressure (Zijlstra & Witte 1985), or as a reflection of variations in the general water circulation pattern (Otto et al. 1990). The trends of increasing water temperature in both the North Sea (Engelhard et al. 2014, <https://www.eea.europa.eu/en/analysis/indicators/european-sea-surface-temperature>) and coastal zone (van Aken 2010) require further analysis of this inverse relationship and the temperature-related underlying processes to enable predicting any future developments in North Sea plaice connectivity. A large-scale field campaign combined with otolith microchemistry (Delerue-Ricard et al. 2019) and microstructure analysis for age to reconstruct time of larval immigration and settling (Karakiri & von Westernhagen 1989, Hovenkamp 1991) is a promising approach for further testing of biophysical modelling predictions. In this respect, it should be kept in mind that there is substantial variability in predictions between models (Hufnagl et al. 2017), which stresses the use of multiple different models instead of relying on only single model predictions, as well as the need for improved observations. Nevertheless, our observational results already confirm some of the main connectivity patterns indicated by such models.

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Appendix. Size-frequency distributions of settled plaice in May as an indicator of annual plaice larval immigration pattern

Data on annual larval immigration pattern and subsequent size-frequency distributions of settled plaice are available for a 3 yr period (1980–1982) for the Balgzand intertidal in the western Dutch Wadden Sea (van der Veer 1986). Larval immigration patterns refer to net immigration calculated as the difference between mean flood and ebb densities. Information of settled plaice are based on a bi-weekly standard monitoring programme at Balgzand, covering 36 hauls. For each haul, numbers caught were corrected for size-selective mesh and catch efficiency and for each mm size class converted into densities per 1000 m². Subsequently, the population size-frequency distribution was calculated as the mean of all hauls. For all 3 years, the size-frequency distributions were calculated for samples at the beginning of May (6 May 1980, 6 May 1981, 10 May 1982)

For all 3 years, the size-frequency distributions were corrected for differences in sampling date and standardised to the date of 7 May. The size-frequency distributions were moved forwards or backwards with the integer of assumed growth rate between the date of sampling and 7 May according to the growth model under excess food for small 0-group plaice (Glazenburg 1983). For details, see Section 2 in the main text. For 1982, sampled on 10 May, the size-frequency distribution was corrected (moved) by 2 mm. Next, due to differences in the number of individuals caught per station, all size-frequency distributions were normalised into relative size-frequency distributions. Finally, for each station and for each year, all relative size-frequency distributions were converted into cumulative

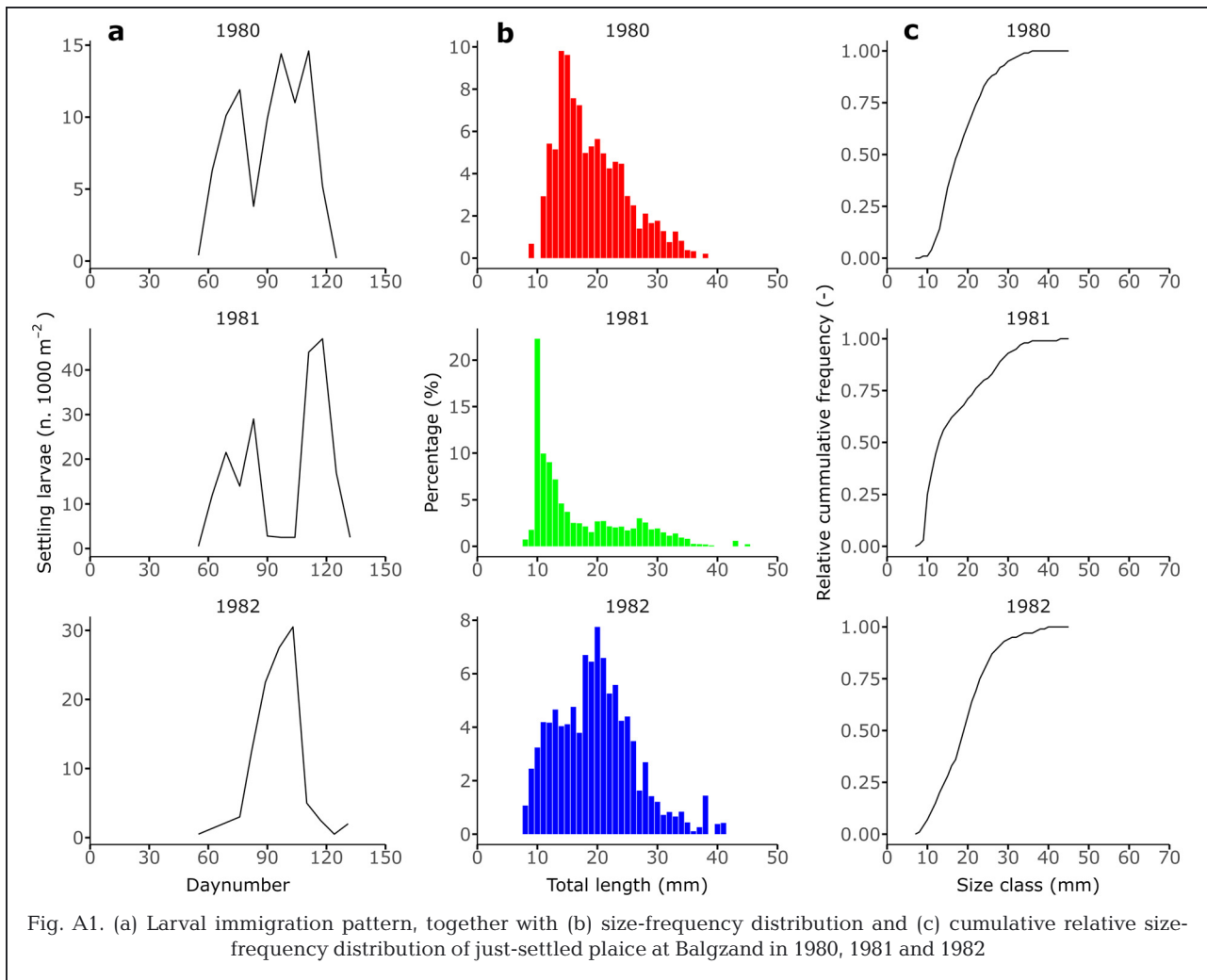
relative size-frequency distributions (CRSFDs) ranging from 0 to 1 (Fig. A1).

For each combination of years, the 2 CRSFDs were compared, and for each size class, the difference in CRSFD was calculated. Next, the maximum difference (largest value) was selected from the resulting distribution. The maximum difference between the 2 CRSFDs was used to apply the Kolmogorov-Smirnov goodness-of-fit test for detecting significant differences between size-frequency distributions: 2 size frequencies are significantly different when the maximum difference exceeds 0.192 at a critical value of 0.05, and 0.231 at a critical value of 0.01 (Chakravarti et al. 1967).

Differences in CRSFD were found between 1981 and both 1980 and 1982. The CRSFDs in 1980 and 1982 were not significantly different from each other (Table A1).

Table A1. Maximum difference between the cumulative relative size-frequency distributions of just-settled plaice in 1980, 1981 and 1982. Significant differences between years according to the Kolmogorov-Smirnov goodness-of-fit test ($p < 0.01$) are highlighted in **bold**

	1980	1981	1982
1980			0.119
1981	0.368		0.318
1982	0.119	0.318	



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