



Size variation of 0-group plaice: Are earlier influences on growth potential a contributing factor?



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ARTICLE INFO

Article history:

Received 29 April 2013

Received in revised form 8 October 2013

Accepted 27 December 2013

Available online 10 January 2014

Keywords:

Pleuronectes platessa

Growth

Abundance

Nursery Grounds

Common garden Rearing

ABSTRACT

Over a decade of sampling has shown that there are consistent differences in the sizes of 0-group plaice by late summer comparing 21 nursery sites on the Scottish west coast. However, when young fish were collected from two sites which produce particularly small and large fish and reared using a common garden design, growth rates between fish from the two sites were indistinguishable. Either there is little selection for fast or slow growth up to a few weeks post-settlement, or such effects do not persist sufficiently strongly to influence later growth. There were also no significant correlations between the time-series of fish size comparing sites, although within some sites there was evidence of inter-annual density-dependent effects. Any influences of offshore regional-scale factors, such as sea temperature or pelagic primary productivity on growth thus appear to be heavily modified by local conditions on the nursery grounds. The field observations combined with the experimental results lead us to conclude that the size 0-group plaice attain in late summer is mainly controlled by post-settlement habitat quality.

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1. Introduction

European plaice (*Pleuronectes platessa* L.) is a commercially important flatfish which has been a focus for fishery research for over a century. Plaice spawning generally commences early in the year and, following a period of planktonic drift, metamorphosing larvae settle into shallow, sandy habitats which are often accessible to researchers (Gibson, 1999). The commercial importance of plaice and the ready accessibility of the nursery grounds explains why so many studies have been undertaken on the post-settlement ecology of plaice, studies which have significantly contributed to our understanding of recruitment dynamics in marine fish (Ciotti, 2012; Nash and Geffen, 2012). An important conclusion from these studies is that fish size and mortality rates are inversely related and that this is generated by predator-prey interactions (Beverton and Iles, 1992a; Ellis and Gibson, 1995; Gibson et al., 1995). Larval and juvenile flatfish growth rates should thus be of key importance in determining overall survival (Ciotti,

2012; Freitas et al., 2012; Teal et al., 2008; van der Veer et al., 2010). Except for the period immediately after settlement (Ciotti et al., 2010, 2013a; Freitas et al., 2012), growth of 0-group plaice appears to be lower than predicted from laboratory experiments (Freitas et al., 2012; van der Veer et al., 2010). The commonest explanation for this is that some form of food limitation is occurring on the nursery grounds. This could result directly from reductions in the abundance or production of prey (Ciotti et al., 2013a), increasing inter-specific competition or declines in food quality (Ciotti, 2012; Freitas et al., 2012; van der Veer et al., 2010). However, there is little clear empirical support for any of these hypotheses. The lack of predictive power of current growth models in relation to field-data (van der Veer et al., 2010) suggests that either some fundamental processes are missing, or that we are not measuring the right factors at appropriate spatial and temporal scales (Ciotti et al., 2013b, 2013c).

The numbers of plaice larvae reaching individual nurseries depends on oceanographic connectivity with the spawning grounds (Bolle et al., 2009; Cushing, 1990; Fox et al., 2006). Plaice spawning on the Scottish west coast has been confirmed in the Clyde Sea by means of plankton surveys (Poxton, 1986) whilst Ellis et al. (2010) and Coull et al. (1998) indicated further spawning grounds to the west of Islay, to the south of Tiree and Coll and to the eastern side of the Isle of Lewis (Fig. 1). Steele and Edwards (1970) also reported a small area of localised spawning between Gairloch and Loch Ewe. Since the prevailing Scottish Coastal Current runs in a northerly direction (Inall et al., 2009), the more

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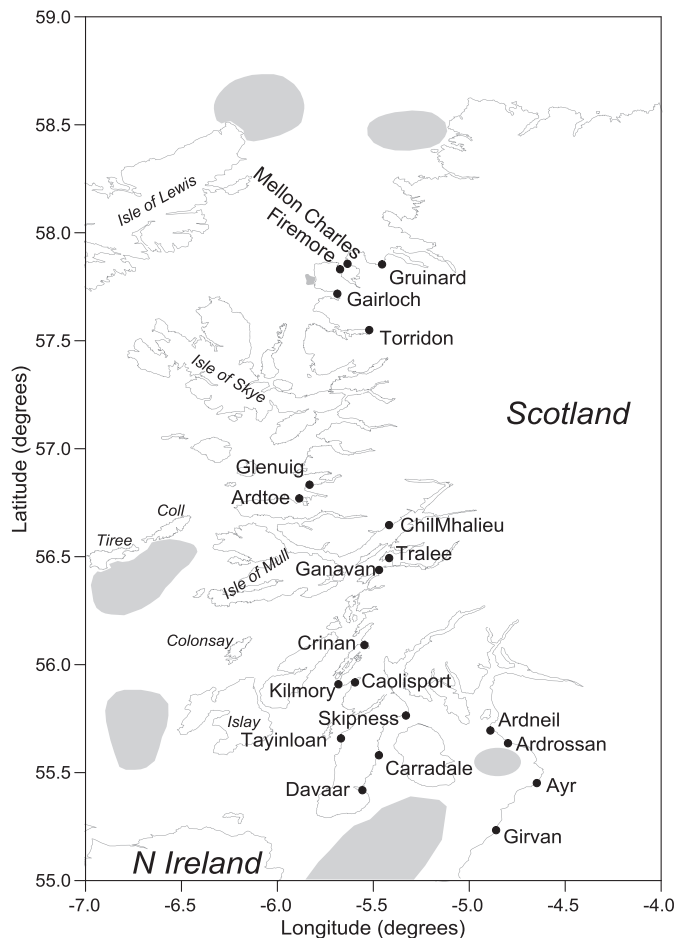


Fig. 1. Locations of the 21 nursery grounds sampled between 2001 and 2011. Shaded areas indicate the locations of plaice spawning grounds reported in the literature.

southern spawning sites may be the source of metamorphosing plaice settling onto beaches along most of the Scottish west coast. Thus, given the variable drift distances of different nurseries from these spawning grounds, there could be potential for growth-rate dependent selection to occur during the planktonic phase. The onset of metamorphosis in flatfish larvae is thought to be related more to size than age (Chambers and Leggett, 1987; Geffen et al., 2007) and, in addition, plaice do not appear to be able to delay settlement while searching for suitable substrates (Gibson and Batty, 1990). Sites further from the spawning grounds might therefore favour settlement of slower growing larvae whilst sites closer to spawning grounds might favour faster growing larvae. If selection for fast- or slow-growing larvae does occur during the planktonic stages, and these differences persist beyond settlement, this could provide an explanation for why faster or slower growing fish tend to be found at certain sites. Growth-dependent selection during the planktonic phase has been demonstrated in anchovy (Takasuka et al., 2004) and mackerel (Dominique et al., 2007) and has been shown to persist beyond larval life in tropical damselfish (Vigliola et al., 2007).

We firstly examined data from surveys conducted each August between 2001 and 2011 at the same twenty-one beaches where 0-group plaice growth has also been estimated using an RNA-based method by Ciotti et al. (2013b). We then tested whether selection for fast or slow-growing fish during earlier life could provide an explanation for the differences in sizes reached in late summer by rearing young post-settlement plaice collected from contrasting sites in a common-garden experiment.

2. Materials and methods

2.1. Beach sampling for size in August, 2001–2011

Juvenile flatfish were sampled at the sites shown in Fig. 1. Four additional locations (Dunstaffnage, Kentra, Shallachen and Loch Sween) were also sampled but were excluded from the data because very low numbers of plaice (<20) were caught at each of these sites in most years. Fish were sampled using 1.5 m beam-trawls towed manually at walking pace for 5 min in water between 0.5 and 1.5 m deep. Three to five replicate tows were completed at each site within 1 h either side of low water. The distance covered by each tow was recorded using hand-held Garmin GPS units. Each trawl had a single spiked tickler chain and 10 mm mesh net and the same trawls were used throughout. Fish were sorted from the catches and anaesthetized using benzocaine or clove oil and then either fixed in 4% formalin or, for years where juvenile plaice were also analysed for molecular condition (2005–2007 only), photographed against a calibration rule before being frozen (Ciotti et al., 2013b). On return to the laboratory, plaice were sorted from the catches and their total lengths (TL) recorded. For fish which had been photographed, lengths were calculated from the calibration rule. Lengths were not adjusted for preservation method as Lockwood (1973) showed that 0-group plaice only shrink by 2.5% when fixed in formalin. For a 50 mm fish this would only make a difference of 1 mm. The density of fish at each site by year was estimated as the total number of fish caught divided by the total swept area. Abundance data were not corrected for net avoidance or gear efficiency (see Discussion). Any plaice caught which were >120 mm TL were assumed to be 1-group survivors from the previous year and were not included in the data analysis.

2.2. Common garden rearing experiments, 2011–2012

To investigate whether 0-group plaice from different sites have inherent growth differences we compared the growth of fish which originated from two sites which have consistently yielded the greatest differences in late-summer size, namely Tralee (56.493°N 005.418°W) which tends to produce larger fish and Caolisport (55.918°N 005.595°W), which tends to produce smaller fish (Fig. 1). In 2011, juvenile plaice (30–60 mm total length) were collected from Caolisport on 27 June and from Tralee on 29 June using the trawl described above (rearing Trial I). Sufficient fish were collected for stocking the experiment plus holding a reserve to replace any mortalities. Fish were transported from the two collection sites to the laboratory in insulated, aerated containers. After 48 h acclimation, fish >35 mm TL were subdermally tagged (ventral surface) using visible-implant-elastomer (VIE, Northwest Marine Technology, Washington, USA) with different colours identifying their site of origin. Using existing data on the typical standard-deviations in size in mid-August, power analysis was used (Faul et al., 2007) to estimate that a total sample size of at least 36 would be needed to detect a difference of 10 mm in final sizes between groups (α probability at 0.95 and β probability at 0.2). Twenty-five fish from each site were therefore assigned to each of three rearing tanks on 1 July ensuring that the initial length distributions of fish from each site within each tank were as equal as possible. The initial size distributions were compared with ANOVA to check that there were no significant differences. Rearing was conducted in 120 l fibreglass tanks with continuous aeration and flow-through seawater. The bottom of each tank was covered with aquarium sand to allow the plaice to undertake their normal burying behaviour. Tanks were cleaned daily and the fish fed *ad libitum* with finely chopped fresh mussel (*Mytilus edulis*). The quantities of mussel offered were increased as the fish grew so that a small amount of uneaten food remained the following morning. Uneaten food was removed using a small hand-net before re-feeding. Water temperature in the tanks was recorded daily. Room lighting was set on a time-cycle of 16:8 h (light:dark) approximating natural conditions at this time of

year and latitude. Fish in the reserve stock were reared under similar conditions. Any fish in the experimental tanks showing signs of disease were removed and replaced with the reserve stock with similar sized fish from the same site. At days 25 and 50, the fish were carefully removed from the experimental tanks using a hand-net, tag identities checked, total lengths measured and the fish returned to cleaned tanks. At day 70, fish were sacrificed using an anaesthetic overdose (150 mg l^{-1}) of MS-222 (Pharmaq, Hampshire, UK) and measured.

In 2012 two further rearing experiments (trials II and III) were undertaken, the first using fish collected earlier in the settlement season and the second repeating the experiment later in the season. Plaice settlement at Tralee and Caolisport was monitored by trawling at the sites every 10 days from mid-April onwards. Towards the end of May it was judged that sufficient settled plaice were being caught for the experiment. Fish were collected on 21–23 May (29–57 mm total length) and moved to the laboratory to acclimate. Fish were VIE tagged on 31st May and groups assigned to rearing tanks on 1st June. The whole procedure was repeated on 22nd–23rd June when collected fish were between 32 and 45 mm in length. Because there was a requirement to have more tanks for trials II and III, tank size had to be reduced to 90 l but otherwise the rearing protocols described above were followed.

2.3. Data analyses

All statistical analyses were performed using R version 2.15.1 (R Development Core Team, 2012). Exploratory data analysis on 0-group plaice size in August across the 21 annually sampled sites was undertaken using summary statistics, smoothed density functions (package 'sm') and box and scatter-plots. Annual size data frequently departed from normal-distributions, and in some cases data were multi-modal, so non-parametric methods were used. Between-site correlations in the time-series of annual median fish size and density were computed using Kendall's rank correlations with the critical significance levels adjusted for multiple comparisons using the Holm–Bonferroni method ('corr.test' from package 'psych'). Between-site comparisons in median size were performed using the Kruskal–Wallis test with the post-hoc multiple comparison from R package 'pgrmess'. Relationships between average plaice density and median fish size at each site were investigated graphically using scatter-plots. Quantile regression was also explored as a potential method for more formally testing these relationships but models failed to fit in many cases, probably due to insufficient degrees-of-freedom.

Fish total lengths from the common garden experiments were firstly log-transformed to stabilise variances and then analysed using mixed linear models following Crawley (2007). This approach takes account of the temporal pseudo-replication within tanks, as it was the same groups of fish which were being measured repeatedly over time ('lme' within R package 'nml'). Tanks (1–3) were treated as replicates within each trial (I–III). This procedure gives improved statistical power against the alternative approach of applying ANOVA on the final size data alone. Growth rates were subsequently modelled using the un-transformed data with generalised least squares ('gls' within R package 'nml') with the option to automatically estimate the variance:mean function in order to account for heteroscedasticity in the data.

3. Results

3.1. Plaice sizes at field sites in August

After adjustment for multiple comparisons, there were no statistically significant between-site correlations for any of the time-series of median fish size in August including geographically adjacent comparisons. However, non-parametric smoothed density estimators of the annual median fish size within sites tended to follow reasonably similar,

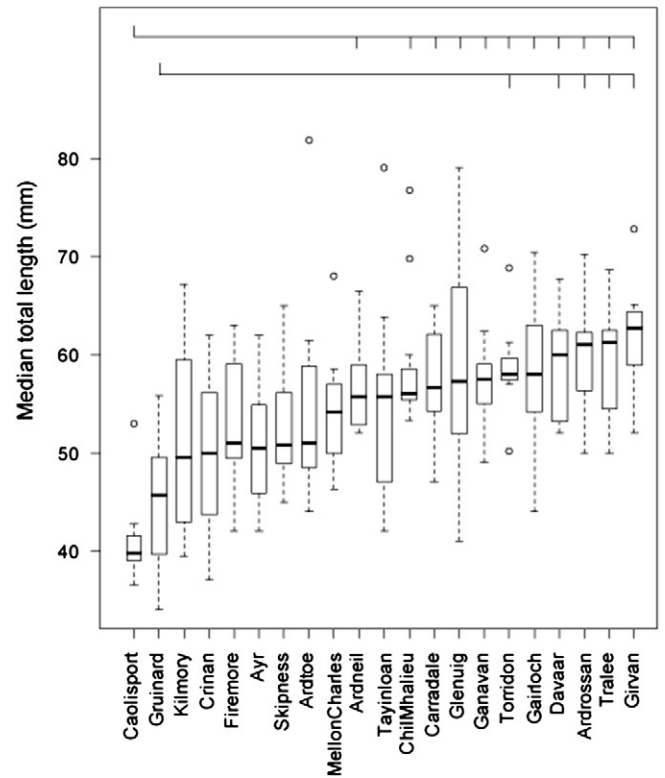


Fig. 2. Distribution of medians of 0-group plaice lengths in August across years (2001–2011). Thickened bar indicates the median; boxes indicate inter-quartile range, dashed lines indicate approximate 95% confidence intervals, circles indicate extreme values. Upper horizontal lines indicate sites where median sizes were statistically different ($p < 0.05$) using the Kruskal–Wallis post-hoc multiple comparison test – tick above indicates which site to compare with others (ticks below).

symmetrical modal distributions (Fig. 2) justifying use of the Kruskal–Wallis test for inter-site comparisons. Median sizes in August (pooled across years) varied significantly between sites (K–W chi-squared = 80.05, $df = 20$, p -value = $3.9e-09$) and were statistically different ($p < 0.05$) when comparing Caolisport and Gruinard with a number of other sites including Tralee and Girvan (Fig. 2). The spread of median sizes over time at each site was least variable at Torrion and Caolisport and most variable at Kilmory and Glenuig. Higher inter-quartile values in Fig. 3 indicate wider size distributions across years whilst a larger spread of values about the median indicates greater variability in the spread of the size distributions over time. Underlying size distributions were thus least variable at Ardtoe and Tralee and most variable at Tayinloan and Glenuig. Statistically significant relationships between median size and inter-quartile range within sites were only found at 5 out of the 21 locations, namely Tayinloan (τ -a = 0.51, $p = 0.047$), Chil Mhalieu (τ -b = 0.60, $p = 0.01$); Glenuig (τ -a = 0.82, $p = 0.0001$); Firemore (τ -a = 0.67, $p = 0.0003$) and Mellon Charles (τ -b = 0.71, $p = 0.003$). These results suggest that sizes of 0-group plaice were consistently small in August at Caolisport while fish at Tralee were amongst the largest. Although fish at Girvan tended to be slightly larger than at Tralee, there was much more inter-annual variability in median size at the former site.

3.2. Plaice densities in August

Median plaice densities were statistically different comparing sites (K–W chi-sq = 48.8, $df = 20$, $p = 0.0033$) with densities at Ayr being significantly higher than Davaar, Gairloch, Firemore and Gruinard (Fig. 4). Densities at Tralee tended to be amongst the highest observed but were quite variable across years resulting in a lack of statistical difference from any of the other sites (Fig. 4). At many sites (amongst

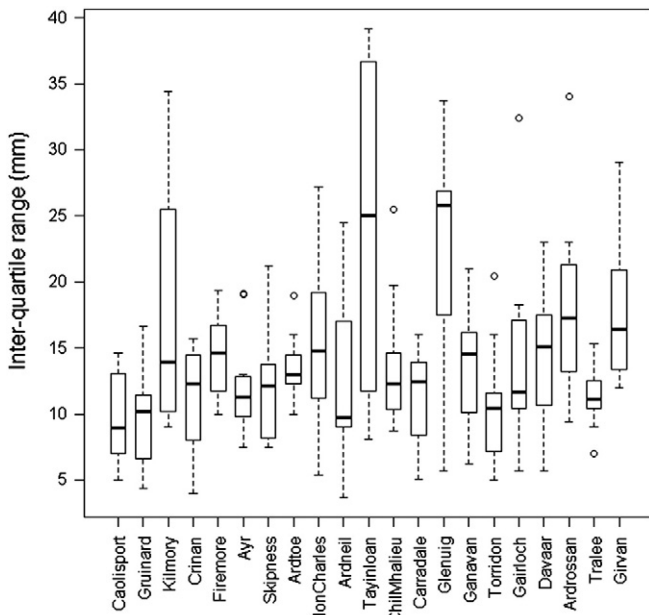


Fig. 3. Distribution of inter-quartile ranges of 0-group plaice lengths in August across years (2001–2011). Thickened bar indicates the median; boxes indicate inter-quartile range, dashed lines indicate approximate 95% confidence intervals, circles indicate extreme values. Site ordering is as in Fig. 2.

years) there were apparent inverse relationships between median size of fish and plaice density (Fig. 5).

3.3. Common garden rearing experiments

In each rearing trial, growth was reasonably linear although the variance increased (Fig. 6). Residuals from fitting mixed linear models to

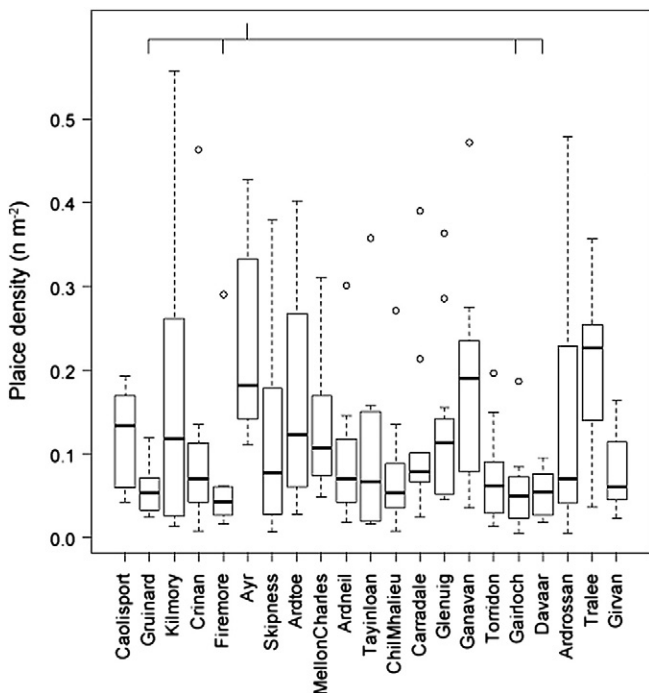


Fig. 4. Boxplots of the distribution of 0-group plaice densities in August across years (2001–2011). Thickened bar indicates the median; boxes indicate inter-quartile range, dashed lines indicate approximate 95% confidence intervals, circles indicate extreme values. Upper horizontal lines indicate sites where median sizes were statistically different ($p < 0.05$) using the Kruskal–Wallis post-hoc multiple comparison test — tick above indicates which site to compare with others (ticks below). Site ordering is as in Fig. 2.

the log-transformed length data were well behaved and model testing indicated that growth in length only varied significantly amongst trials (Table 1). There was no evidence that fish from Caolisport and Tralee had different inherent growth potentials, nor were interactions between rearing tank and origin of the fish significant (Fig. 6 and Table 1). These conclusions held regardless of whether the experimental fish had been collected earlier or later in the season. Linear growth rates (Table 2) were higher in Trial I (0.50 mm day^{-1}) than in Trial II (0.38 mm day^{-1}) or Trial III (0.43 mm day^{-1}). In the 2011 rearing experiment water temperatures rose from around $13.3 \text{ }^{\circ}\text{C}$ to $14.5 \text{ }^{\circ}\text{C}$ by the end of the experiment whilst in 2012, temperatures in Trial II were initially slightly lower (around $12.8 \text{ }^{\circ}\text{C}$) but reached just over $14 \text{ }^{\circ}\text{C}$ at the end. In Trial III, temperatures started around $13.3 \text{ }^{\circ}\text{C}$ and increased to $15.5 \text{ }^{\circ}\text{C}$ (Fig. 7). Post-tagging mortalities during Trial I were low at 3% over the 70 days but in 2012 mortalities were higher (21% in Trial II and 15% in Trial III). This was possibly related to using smaller tank sizes in the 2012 experiments.

4. Discussion

Plaice nursery sites along the Scottish west coast had a consistent rank order in terms of the size 0-group fish attained by late summer over the 11 years sampled. In particular, Caolisport and Guinard tended to produce small fish, whilst Tralee and Girvan produced larger fish. Although density-dependence played a role in controlling inter-annual differences in fish size within some sites, it did not explain the differences in fish size between these extreme sites. We were also unable to detect any significant correlations comparing the time-series of August 0-group plaice size for sites with each other. Each site thus appears to be behaving largely independently, and we interpret this as evidence that size achieved by late summer is controlled by the underlying habitat quality of each nursery ground. These conclusions are broadly in accord with Ciotti et al. (2013b) who detected high variability in RNA-predicted recent growth rates at the 25 km scale. Recent growth was also significantly related to plaice density but also to regional-scale physical factors such as wave exposure and tidal range (Ciotti et al. 2013b). There are a number of reasons why long-term patterns in size between sites in August (this study) might not correspond with spatial patterns in RNA-predicted recent growth including differences in the lengths of the time-series used (11 years compared with 3), disconnect between late summer recent growth rates and late summer achieved size or differences in the statistical methods applied. A useful next step would be to perform further mixed modelling to investigate whether spatial patterns of cumulative seasonal growth (present study) correspond with recent growth estimates in late summer measured across the same sites (Ciotti et al., 2013b).

In our common garden rearing experiments, 0-group plaice collected from Tralee and Caolisport failed to show any statistical differences in growth. The number of fish used in the each trial along with the amount of replication (3 replicates by 3 trials including fish collected at different times through the settlement season) should have delivered a statistical power of at least 0.8. However, we were unable to fully separate pre- and post-settlement phases as the fish used to populate our experiments would have been up to several weeks post-settlement (based on their size and expected growth rates in the field). Unfortunately in a pilot study we found that VIE tagging plaice $< 35 \text{ mm TL}$ led to significant post-tagging mortality. We cannot therefore categorically rule out the possibility that batches of larvae selected for fast- or slow growth during the planktonic phase are delivered to specific nurseries, or that growth rate selection does occur during settlement, but the evidence suggests that either this does not occur, or that the effects of any such selection do not persist beyond a few weeks of growth on the nursery grounds. Had our common garden rearing revealed significant site effects on growth it would have been worth repeating the experiments using smaller fish closer to settlement size in order to try and pin-point the stage at which such effects appear. Such small fish

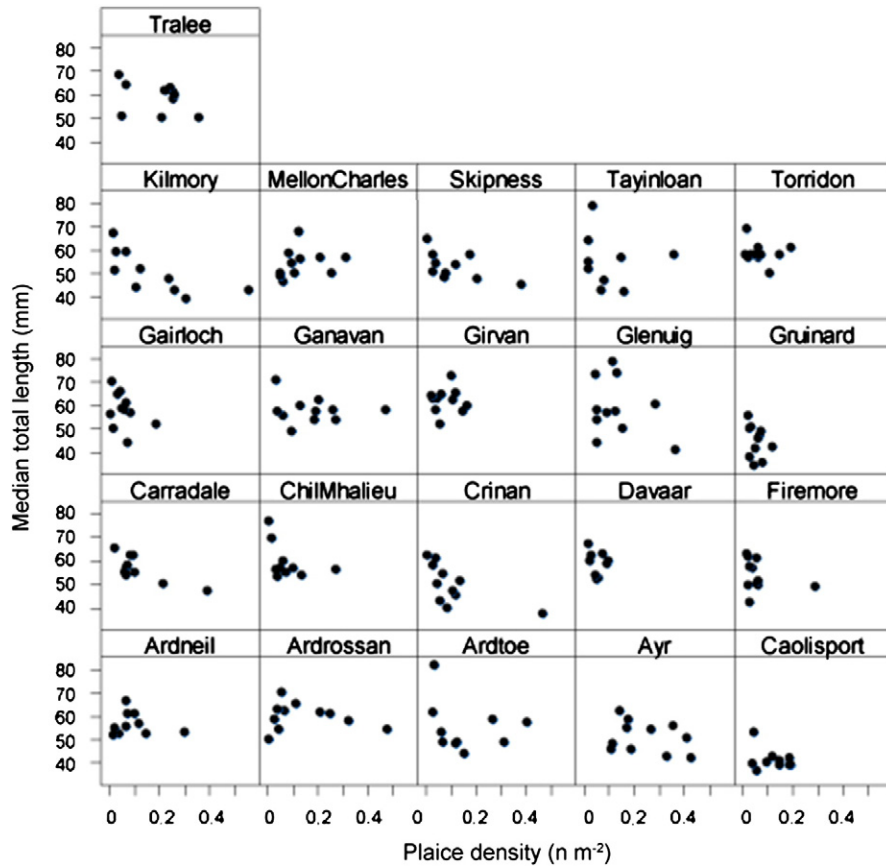


Fig. 5. Median length of 0-group plaice August vs. density at each site (based on 11 years of sampling 2001–2011). At a few sites no fish were caught in some years so the number of points shown in each panel can be less than 11.

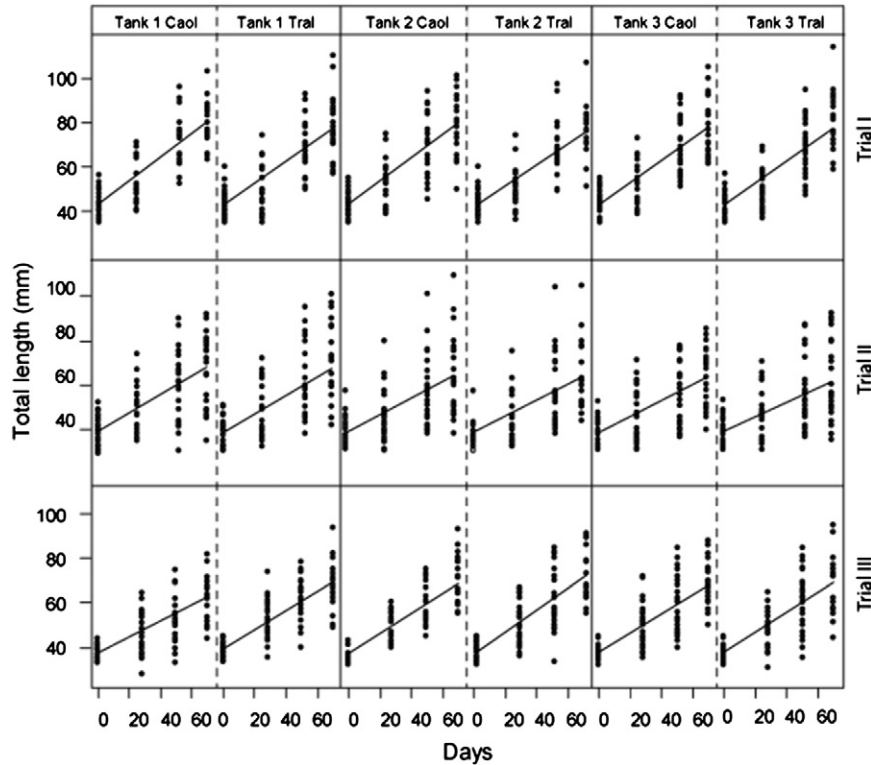


Fig. 6. Changes in length of experimentally reared 0-group plaice during the common garden rearing experiments. Caol indicates fish originating from Caolisport, Tral indicates fish originating from Tralee. Dots indicate sizes of individual fish; lines are fitted linear growth rates to each site group within each tank.

Table 1

Results of mixed modelling of the common garden rearing results – only fixed effects reported – site nested within tank nested within trial.

Fixed effect	Value	Std. error	DF	t-value	p-value
(intercept)	1.64	0.0062	1746	266.62	<0.001
Trial	−0.024	0.0044	1746	−5.39	<0.001
trial:tank	−0.0086	0.0018	1746	−0.47	0.64
trial:tank:site	0.00038	0.00087	1746	0.44	0.66

would have to be tagged using an alternate approach, for example immersion in a seawater solution of fluorescent-dye which becomes incorporated into the otoliths (Liu et al., 2009). We chose not to use this method for two reasons. Firstly the fish from the two sites would not receive identical marking treatments – one group would need to be immersion-marked whilst the other would not and it is known that immersion marking can lead to short-term reductions in growth. Perhaps more importantly distinguishing otolith-marked from un-marked fish can only be achieved by removing the otoliths after the fish are killed and then examining them using ultra-violet epifluorescence microscopy. This would mean that fish sizes recorded during the rearing experiments could not be assigned to the origin sites so that the statistical analysis would reduce to an ANOVA on final sizes – a less powerful approach than the repeated-measures design used.

In our rearing trials the mean growth rates (0.38 to 0.50 mm day^{−1}) were lower than those reported by Fonds et al. (1992) at similar temperatures and diet (0.64 mm day^{−1}). These differences could be due to the smaller tanks used in the present study which may have increased competition between fish resulting in slower growth for some individuals. Despite the lower average growth, the final sizes of the fish in our rearing experiments were at least as large as those found in August at the field sites (Fig. 2).

We did see evidence for density-dependent effects on August fish size at some, but not all, of the field sites. Negative relationships between the size of 0-group plaice and their abundance in late summer have been reported from a number of nursery grounds (Geffen et al., 2011; Nash et al., 2007; Rauck and Zijstra, 1978; Zijlstra and Witte, 1982; Zijlstra et al., 1982). The obvious explanation for such relationships is that growth becomes food-limited when plaice densities are high (intraspecific competition). However, Kuipers (1977) working in the Wadden Sea, demonstrated that because of high production to consumption ratios, food limitation at that site was unlikely. Zijlstra and Witte (1982) further showed that juvenile plaice growth rates at that location were consistent with a simple temperature-dependent model based on *ad libitum* feeding experiments. They re-interpreted the field-data as indicating that the size-abundance effect actually arose as a consequence of sea temperatures during the planktonic phase. Low temperatures would both encourage larger year-classes and lead to later settlement, and thus smaller sizes during the summer (van der Veer, 1986). However, this explanation appears somewhat unlikely when comparing proximate sites along the Scottish west coast since the fish should have experienced similar sea temperatures during

Table 2

Results of linear models fit to the common garden rearing data pooled by trial. Reported var. func. is the power relationship to the mean which has been estimated to deal with the heteroscedasticity in the data.

Trial		Value	Std. error	t-value	p-value
I	var. func.	1.38			
	(intercept)	41.98	0.49	85.70	<0.001
	slope	0.50	0.02	31.08	<0.001
II	var. func.	1.84			
	(intercept)	38.11	0.52	72.85	<0.001
	slope	0.38	0.02	21.14	<0.001
III	var. func.	2.08			
	(intercept)	37.63	0.33	112.41	<0.001
	slope	0.43	0.01	33.07	<0.001

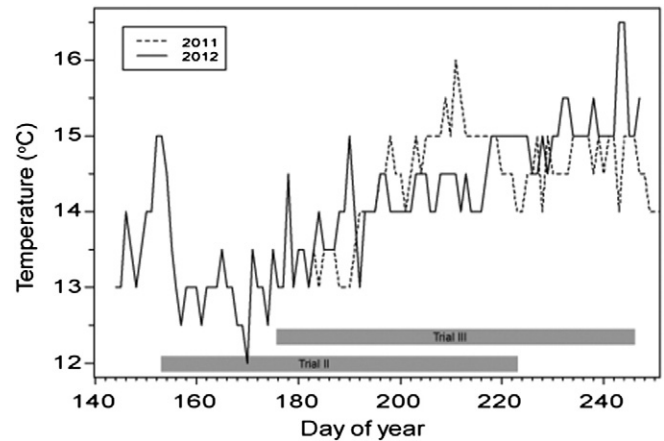


Fig. 7. Daily water temperatures during the acclimation periods and rearing experiments. In 2011 there was a single experiment covering the whole period shown (dashed line). For 2012 the light grey bars indicate the duration of Trials II and III.

their planktonic phase. The studies cited, including the present results, show that density-dependent growth is a feasible but by no means universal (Haynes et al., 2012) phenomenon on plaice nursery grounds. Whether it occurs at a particular site is presumably the result of the range of settlement intensity experienced (Nash et al., 2007) interacting with the local carrying capacity.

The lack of any significant correlations between the time-series of 0-group plaice densities in August comparing sites is somewhat surprising. It is known that at larger regional-scales, time-series of plaice recruitment (measured at age 1) are correlated and that this appears to be driven by sea temperatures experienced during the previous Feb–June (Fox et al., 2000). Since strong plaice year-classes are thought to be generated during the planktonic phase, one might expect year-class variability to be apparent on the nursery grounds, and to show a degree of regional coherence. However, in Loch Ewe (Scotland), Steele and Edwards (1970) reported that the abundance ranking across years at settlement had changed by late summer and similar conclusions were reached for the Irish Sea by Nash and Geffen (2000). In the North Sea, the abundance of 0-group plaice in the English nurseries did not reflect subsequent year-class strength at all (Whiting, 1983) although the abundance in the Wadden Sea, which is thought to contribute the majority of recruits to the southern North Sea stock, did (Rauck and Zijstra, 1978). This spatially fine-scaled variability was captured by Beverton and Iles (1992b) in the concept of a parental stock being linked to a large number of ‘mini-nurseries’, each with differing functional attributes. Both settlement intensity and late summer densities may thus be substantially modified by local conditions (Haynes et al., 2012; Wennhage et al., 2007) and links between 0-group plaice abundance and subsequent recruitment to adult stocks may not be apparent at many individual nursery grounds.

In the present study, 0-group plaice were sampled each August using beam-trawls, towed parallel to the shore in shallow water (<1.5 m depth). This method was used for logistical reasons as several sites often had to be sampled in one day. This approach could have biased the resulting fish length data by failing to capture larger 0-group fish which had already moved into deeper water (Geffen et al., 2011; Gibson et al., 1996). However, Lockwood (1974) found that larger plaice (>40 mm) only start to move out of the shallows at the end of August and at Tralee, Gibson et al. (2002) showed that the median depth for 0-group plaice is usually 1 m until mid-September. Sampling was also undertaken around low water when fish should be concentrated in the shallows. However, growth- or size-related emigration has not been studied at sites other than Tralee on the Scottish west coast so differences between sites, or changes in emigration patterns over time, could have contributed to observed differences in fish size. Long-term changes in the patterns of emigration of juvenile plaice have been

noted in the southern North Sea and are thought to be related to increasing summer water temperatures (van Keeken et al., 2007). However, summer temperatures in the inshore waters to the west of Scotland have not increased during the years of our study, although this did follow a period of increase between 1980 and 2000 (Fox and Howe, 2011; Inall et al., 2009). Estimates of fish population abundance and size can also be biased by changes in catch efficiencies. Edwards and Steele (1968) showed that the Riley type 2 m beam trawl had a fixed efficiency of around 32% for plaice from 25 to 80 mm in length. However, using enclosure experiments, Kuipers (1975) showed that the efficiency of the Dutch 2 m beam trawl declines from around 100%, when juvenile plaice are 50 mm length, to around 35% by the time fish reach 125 mm. We did not attempt to correct our catch-at-size data using size-variable factors (Kuipers et al., 1992) because the corrections depend on such a large number of interacting factors including trawl design and rigging, towing speed, seabed type, sea-state and time of day. Although this approach is in line with other studies on 0-group plaice (Burrows et al., 2001; Ciotti et al., 2013c), further experiments on the catch efficiency of the 1.5 m beam trawl would be useful.

Plaice typically arrive at nursery grounds over a period of several weeks and in some cases settlement of distinct cohorts has been observed (Al-Hossaini et al., 1989; Geffen et al., 2011). Variable timing in settlement is recognised as a complicating factor when comparing size distributions between sites later in the year. Although this might have contributed to the differences we observed, Ciotti et al. (2010) also showed that recent individual growth rates (estimated using an RNA-based method) were significantly lower at Caolisport, compared with Tralee, from as early as mid-July. Individual growth rates at Caolisport were low throughout the summer, but at Tralee growth only dropped to a similar low level at the end of August (Ciotti et al., 2010). Such *in situ* measurements of recent growth support the conclusions based on sizes reached in August presented here.

Our field results, along with those presented in Ciotti et al. (2010, 2013a, 2013b, 2013c), suggest that the sizes attained by 0-group plaice in late summer on the Scottish west coast are the result of differences in local nursery ground quality. Results from the common garden rearing experiments suggest that either there is no selection for growth-traits at earlier stages (when plaice are <40 mm TL), or if such selection does occur, that the effects do not persist sufficiently to affect the growth potential of the fish during the spring and summer. Further research is required at selected sites to elucidate the mechanisms controlling juvenile plaice growth bearing in mind that differences in the timing of settlement might also be important. Physical factors, such as tidal range and wave exposure, appear to be significant (Ciotti et al., 2013b) and could be acting via effects on individual fish behaviour, for example by limiting the spatial scope for foraging. At present links between individual behaviour and realised growth are difficult to investigate because the movements of individual fish within nursery grounds cannot be tracked over long periods of time (Burrows et al., 1994). Advances in readable tag technology which might achieve this should be investigated further.

Acknowledgements

A large team of people helped collect the time-series data, in particular L. Ault; R. Batty; C. Beveridge; R. Gray; R. Harvey; S. Houcutt; S. Heymans; L. Robb and G. Twigg. Rearing experiments were conducted under UK Home Office Project licence 60/4223. The project was partially funded by Oceans 2025 Theme 4 of UK Natural Environmental Research Council (NERC), T. Targett's travel was supported by NERC's Oceans 2025 Program (Theme 4), by the Association of European Marine Biological Laboratories access to infrastructure project (ASSEMBLE) and by the University of Delaware. L. Hortsmeyer and K. de Kroon were supported by EU Erasmus and Van Hall Larenstein University exchange programmes and B Ciotti by a Research Bursary (awarded to B.J.C. and T.E.T.) from the Scottish Association for Marine Science and a

Barbara Prosser Graduate Student Research Award from the University of Delaware.

References

- Al-Hossaini, M., Liu, Q., Pitcher, T.J., 1989. Otolith microstructure indicating growth and mortality among plaice, *Pleuronectes platessa* L., post-larval sub-cohorts. *J. Fish Biol.* 35 (Suppl. A), 81–90.
- Beverton, R.J.H., Iles, T.C., 1992a. Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters II. Comparison of mortality rates and construction of life table for 0-group plaice. *Neth. J. Sea Res.* 29, 49–59.
- Beverton, R.J.H., Iles, T.C., 1992b. Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters III. Density-dependence of mortality rates of 0-group plaice and some demographic implications. *Neth. J. Sea Res.* 29, 61–79.
- Bolle, L.J., Dickey-Collas, M., van Beek, J.K.L., Erftemeijer, P.L.A., Witte, J.I.J., van der Veer, H.W., Rijnsdorp, A.D., 2009. Variability in transport of fish eggs and larvae III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. *Mar. Ecol. Prog. Ser.* 390, 195–211.
- Burrows, M.T., Gibson, R.N., Robb, L., Comely, C.A., 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *J. Exp. Mar. Biol. Ecol.* 177, 251–268.
- Burrows, M.T., Gontarek, S.J., Nash, R.D.M., Gibson, R.N., 2001. Shrimp predation on 0-group plaice: contrasts between field data and predictions of an individual-based model. *J. Sea Res.* 45, 243–254.
- Chambers, C.R., Leggett, W.C., 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. *Can. J. Fish. Aquat. Sci.* 44, 1936–1947.
- Ciotti, B.J., 2012. Patterns and Causes of Spatial and Temporal Variation in Growth Rates of Early Juvenile European Plaice. University of Delaware, Delaware (PhD: 296).
- Ciotti, B.J., Targett, T.E., Nash, R.D.M., Batty, R.S., Burrows, M.T., Geffen, A.J., 2010. Development, validation and field application of an RNA-based growth index in juvenile plaice *Pleuronectes platessa*. *J. Fish Biol.* 77, 2181–2209.
- Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013a. Decline in growth rates of juvenile European plaice (*Pleuronectes platessa*) during summer at nursery beaches along the west coast of Scotland. *Can. J. Aquat. Sci.* 70, 720–734.
- Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013b. Spatial variation in growth rate of early juvenile European plaice *Pleuronectes platessa*. *Mar. Ecol. Prog. Ser.* 475, 213–232.
- Ciotti, B.J., Targett, T.E., Nash, R.D., Burrows, M.T., 2013c. Small-scale spatial and temporal heterogeneity in growth and condition of juvenile fish on sandy beaches. *J. Exp. Mar. Biol. Ecol.* 448, 346–359.
- Coull, K.A., Johnstone, R., Rogers, S.I., 1998. Fisheries Sensitivity Maps in British Waters. UKOAA Ltd.
- Crawley, M.J., 2007. The R Book. John Wiley and Sons Ltd., Chichester (Pages pp.).
- Cushing, D.H., 1990. Hydrographic containment of a spawning group of plaice in the Southern Bight of the North Sea. *Mar. Ecol. Prog. Ser.* 58, 287–297.
- Dominique, R., Castonguay, M., Fortier, L., 2007. Early growth and recruitment in Atlantic mackerel *Scomber scombrus*: discriminating the effects of fast growth and selection for fast growth. *Mar. Ecol. Prog. Ser.* 337, 209–219.
- Edwards, R., Steele, J.H., 1968. The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. *J. Exp. Mar. Biol. Ecol.* 2, 215–238.
- Ellis, T., Gibson, R.N., 1995. Size-selective predation of 0-group flatfishes on a Scottish coastal nursery ground. *Mar. Ecol. Prog. Ser.* 127, 27–37.
- Ellis, J.R., Milligan, S., Readdy, L., South, A., Taylor, N., Brown, M., 2010. MB5301 mapping spawning and nursery areas of species to be considered in marine protected areas (marine conservation zones). Report No 1: Final Report on development of derived data layers for 40 mobile species considered to be of conservation importance. Cefas, Lowestoft, p. 96.
- Faul, F., Erdfelder, E., Lang, A.-G., Buchner, A., 2007. G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav. Res. Methods* 39, 175–191.
- Fonds, M., Cronie, R., Vethaak, A.D., van der Puyl, P., 1992. Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Neth. J. Sea Res.* 29, 127–143.
- Fox, C.J., Howe, J., 2011. The physical and biological environment. In: Bailey, N., Bailey, D.M., Bellini, L.C., Fernandes, P.G., Fox, C., Heymans, S., Holmes, S., Howe, J., Hughes, S., Magill, S., McIntyre, F., McKee, D., Ryan, M.R., Smith, I.P., Tyldesley, G., Watret, R., Turrell, W.R. (Eds.), The West of Scotland Marine Ecosystem: A Review of Scientific Knowledge Marine Scotland Science Report Scottish Government, Aberdeen, pp. 18–59.
- Fox, C.J., Planque, B., Darby, C.D., 2000. Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L.) around the United Kingdom and the influence of sea temperature. *J. Sea Res.* 44, 159–168.
- Fox, C., McCloghrie, P., Young, E.F., Nash, R.D.M., 2006. The importance of individual behaviour for successful settlement in juvenile plaice – a modelling and field study in the eastern Irish Sea. *Fish. Oceanogr.* 15, 301–313.
- Freitas, V., Kooijman, S.A.L.M., van der Veer, H.W., 2012. Latitudinal trends in habitat quality of shallow water flatfish nurseries. *Mar. Ecol. Prog. Ser.* 471, 203–214.
- Geffen, A.J., van der Veer, H.W., Nash, R.D.M., 2007. The cost of metamorphosis in flatfishes. *J. Sea Res.* 58, 35–45.
- Geffen, A.J., Nash, R.D.M., Dau, K., Harwood, A.J.P., 2011. Sub-cohort dynamics of 0-group plaice, *Pleuronectes platessa* L., in the Northern Irish Sea: Settlement, growth and mortality. *J. Exp. Mar. Biol. Ecol.* 400, 108–119.

- Gibson, R.N., 1999. The ecology of the early life stages of the plaice, *Pleuronectes platessa* L: a review. Bull. Tohoku Natl. Fish. Res. Inst. 62, 17–50.
- Gibson, R.N., Batty, R.S., 1990. Lack of substratum effect on the growth and metamorphosis of larval plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 66, 219–223.
- Gibson, R.N., Yin, M.C., Robb, L., 1995. The behavioural basis of predator–prey size relationships between shrimp (*Crangon crangon*) and juvenile plaice (*Pleuronectes platessa*). J. Mar. Biol. Assoc. U. K. 75, 337–349.
- Gibson, R.N., Robb, L., Burrows, M.T., Ansell, A.D., 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. Mar. Ecol. Prog. Ser. 130, 1–17.
- Gibson, R.N., Robb, L., Wennhage, H., Burrows, M.T., 2002. Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. Mar. Ecol. Prog. Ser. 229, 233–244.
- Haynes, P.S., Brophy, D., McGrath, D., 2012. Variability in the early life stages of juvenile plaice (*Pleuronectes platessa*) on west of Ireland nursery grounds: 2000–2007. J. Mar. Biol. Assoc. U. K. 92, 395–406.
- Inall, M., Gillibrand, P., Griffiths, C., MacDougal, N., Blackwell, K., 2009. On the oceanographic variability of the North-West European Shelf to the West of Scotland. J. Mar. Syst. 77, 210–226.
- Kuipers, B., 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). Neth. J. Sea Res. 9, 69–85.
- Kuipers, B.R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. Neth. J. Sea Res. 11, 56–91.
- Kuipers, B.R., MacCurrin, B., Miller, J.M., van der Veer, H.W., Witte, J.J., 1992. Small trawls in juvenile flatfish research – their development and efficiency. Neth. J. Sea Res. 29, 109–117.
- Liu, Q., Zhang, X.M., Zhang, P.D., Nwafili, S.A., 2009. The use of alizarin red S and alizarin complexone for immersion marking Japanese flounder *Paralichthys olivaceus* (T.). Fish. Res. 98, 67–74.
- Lockwood, S.J., 1973. Weight and length changes of 0-group plaice (*Pleuronectes platessa* L.) after preservation in 4% neutral formalin. J. Cons. Int. Explor. Mer 35, 100–101.
- Lockwood, S., 1974. The settlement, distribution and movements of 0-group plaice *Pleuronectes platessa* (L.) in Filey Bay, Yorkshire. J. Fish Biol. 6, 465–477.
- Nash, R.D.M., Geffen, A.J., 2000. The influence of nursery ground processes in the determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. J. Sea Res. 44, 101–110.
- Nash, R.D.M., Geffen, A.J., 2012. Mortality through the early life-history of fish: what can we learn from European plaice (*Pleuronectes platessa* L.)? J. Mar. Syst. 93, 58–68.
- Nash, R.D.M., Geffen, A., Burrows, M.T., Gibson, R.N., 2007. Dynamics of shallow-water juvenile flatfish nursery grounds: application of the self-thinning rule. Mar. Ecol. Prog. Ser. 344, 231–244.
- Poxton, M.G., 1986. The distribution of plaice eggs and larvae in the Clyde Sea area. Proc. R. Soc. Edinb. 90B, 491–499.
- R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rauk, G., Zijstra, J.J., 1978. On the nursery-aspects of the Waddensea for some commercial fish species and possible long-term changes. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 172, 266–275.
- Steele, J.H., Edwards, R.R.C., 1970. The ecology of 0-group plaice and common dabs in Loch Ewe, IV. Dynamics of the plaice and dab populations. J. Exp. Mar. Biol. Ecol. 4, 174–187.
- Takasuka, A., Oozeki, Y., Kimura, R., Kubota, H., Aoki, I., 2004. Growth-selective predation hypothesis revisited for larval anchovy in offshore waters: cannibalism by juveniles versus predation by skipjack tunas. Mar. Ecol. Prog. Ser. 278, 297–302.
- Teal, L.R., Leeuw, J.J.d, van der Veer, H.W., Rijnsdorp, A.D., 2008. Effects of climate change on growth of 0-group sole and plaice. Mar. Ecol. Prog. Ser. 358, 219–230.
- van der Veer, H.W., 1986. Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29, 223–236.
- van der Veer, H.W., Freitas, V., Koot, J., Witte, J.J., Zuur, A.F., 2010. Food limitation in epibenthic species in temperate intertidal systems in summer: analysis of 0-group plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 416, 215–227.
- van Keeken, O.A., van Hoppe, M., Grift, R.E., Rijnsdorp, A.D., 2007. Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. J. Sea Res. 57, 187–197.
- Vigliola, L., Doherty, P.J., Meekan, M.G., Drown, D.M., Jones, E.M., Barber, P.H., 2007. Genetic identity determines risk of post-settlement mortality of a marine fish. Ecology 88, 1263–1277.
- Wennhage, H., Pihl, L., Stål, J., 2007. Distribution and quality of plaice (*Pleuronectes platessa*) nursery grounds on the Swedish west coast. J. Sea Res. 57, 218–229.
- Whiting, C.L., 1983. Plaice, sole and turbot year-class strength estimates. Ann. Biol. 40, 152–155.
- Zijlstra, J.J., Witte, J.Y., 1982. On the relation between length and abundance in 0-group plaice of the North Sea. International Council for the Exploration of the Sea, C.M. 1982/G:4.
- Zijlstra, J.J., Dapper, R., Witte, J.J., 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the Western Wadden Sea. Neth. J. Sea Res. 15, 250–272.