



Field experiments on depth selection by juvenile plaice *Pleuronectes platessa*

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ABSTRACT: After settlement on sandy beaches in spring, juvenile (0-group) plaice *Pleuronectes platessa* L. spend the summer and autumn months at depths <5 m. During this time, there is a strong length–depth relationship in which the smaller fish are most common at the shallow end of their depth range. Mark and recapture experiments with fish caught at depths of 0.5 and 2.5 m demonstrated that nearly all fish subsequently released at their depth of capture stayed at that depth, and few moved to other depths. In contrast, many fish reciprocally transplanted between these depths returned to their depth of capture within 2 d, and very few remained at the transplant depth. The results indicate that juvenile plaice have a fidelity to, and can actively select, a particular depth, although there may be some movement between depths, most of which at the time of the experiment (August/September) was directed offshore.

KEY WORDS: Plaice · *Pleuronectes platessa* · Depth distribution · Depth fidelity · Homing · Habitat selection

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INTRODUCTION

Shallow coastal waters often act as nursery grounds for juvenile fishes and invertebrates because they optimise growth and minimise mortality of the vulnerable young stages. In northwest European waters, plaice *Pleuronectes platessa* L. are common and often numerically dominant members of the benthic ichthyofauna on sandy shores (Gibson et al. 1993, Beyst et al. 2001). Plaice spawn offshore early in the year, and their larvae are transported shoreward by a combination of drift and active migration (Creutzberg et al. 1978, Rijnsdorp et al. 1985, Bergman et al. 1989, Fox et al. 2006). When close to shore, the planktonic larvae metamorphose and in spring settle on the sea bed in sandy areas to take up their juvenile benthic life style. Once settlement is complete, the newly arrived plaice population is mostly concentrated at depths of <5 m, and this distribution remains essentially stable until autumn. Although the summer distribution is stable and the population is distributed between the water's edge and the outer limit of ~5 m, individuals are not uniformly distributed within this depth range. Instead,

the maximum abundance occurs at 1 to 2 m. This unequal distribution is caused by an underlying length–depth relationship (Bregneballe 1961, Edwards & Steele 1968, Gibson 1973, Kuipers 1973, Gibson et al. 2002) in which mean length increases with depth. Because the length–frequency distribution is approximately normal, peak density occurs at the depth occupied by those fish close to the mean length. It is also a feature of this distribution that, although larger individuals in the population can be found at all depths within the range, the smallest individuals are absent from deeper water (Gibson et al. 2002). This general pattern of variation in length and abundance with depth is common but not universal. In the North Frisian Wadden Sea, for example, the length–frequency distribution of the population becomes bimodal with time. In this case, the larger, faster-growing fish are found in shallower water than the smaller, slower-growing ones (Bergmann 1987). The positive relationship between depth and length–abundance is not as clear in populations inhabiting very shallow water (~1 m), but even here there is usually a relationship between abundance and distance from the shoreline (Modin & Pihl 1996). This

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length–depth relationship on the nursery ground represents the innermost end of a wider distribution of all length classes initially described for plaice by Heincke (1905) and subsequently known as Heincke's law. It represents an example of a wider length–depth relationship described for many (Macpherson & Duarte 1991, Labropoulou et al. 2008) but not all (e.g. Stefanescu et al. 1992) fish species. Superimposed on this general pattern of depth distribution, however, are changes in distribution over both short and longer time scales. On beaches where there is a significant tidal range, young plaice undertake onshore/offshore tidal migrations (Gibson 1973, Kuipers 1973, van der Veer & Bergman 1986, Burrows et al. 1994, Gibson et al. 1996). Where tidal range is small, no such tidally-related movements can be detected, but in both tidal and non-tidal areas, the fish move into shallower water at night (Gibson et al. 1998). These tidal and diel movements continue throughout the summer, but in autumn there is a gradual emigration into deeper water (Hill 1971, Gibson 1973, Lockwood 1974, Poxton et al. 1983).

The observed length–depth relationship could have several, not necessarily exclusive, explanations. It may be caused by differential depth-related growth such that fish in deeper water grow faster than those in shallow water. It could also be related to predation pressure because it is known that predators are more numerous and more varied in deeper water (Ellis & Gibson 1995) and that vulnerability to predators is size related (van der Veer & Bergman 1987, Ellis & Gibson 1995, 1997, Gibson et al. 1995). Consequently, the smaller fish in that part of the population inhabiting deeper water would experience higher predation rates than larger fish. Superimposed on these 2 indirect effects is the possibility that individual fish can actively select, and maintain their position at, a specific depth. Larger fishes may be found in deeper water as a consequence of increased preferred depth with increasing size (Gibson et al. 2002). This paper describes the results of a study designed to examine this possibility. A field experiment was carried out in which marked fish were either released at their depth of capture or transplanted to another depth. A subsequent sampling programme enabled the movements of fish to be followed after marking to examine whether fish have an innate depth preference, maintain their position at the preferred depth, and return to that depth if transplanted.

MATERIALS AND METHODS

Capture methods. The experiments were carried out on the sandy Tralee beach in Ardmucknish Bay, Argyll, Scotland. The benthic ichthyofauna of this beach,

which is dominated numerically by juvenile plaice, has been extensively studied in previous investigations (e.g. see Gibson et al. 1993, 1996), and the beach is described in detail in those studies. The fish used were caught with a 1.5 m beam trawl pulled by hand at a depth of 0.5 m and a 2 m beam trawl using a small boat and outboard at 2.5 m depth at 2 stations (A and B) ~360 m apart. The distance between the 2 depths was ~100 m at each station. Each trawl tow was made parallel to the beach within ± 2 h of low tide and lasted 4 min. The catch from each haul was transferred to a large shallow plastic container filled with seawater and taken to the marking station on the beach. The plaice in the hauls were carefully picked out from the plastic containers and transferred to buckets of seawater aerated with a battery-driven pump. The initial marking and release was carried out over 4 d in August 1996: at Stn A on Days 1 and 3 and at Stn B on Days 2 and 4.

Marking methods. Mark effect trials: Prior to the field experiments, 200 fish from 0.5 m and 166 from 2.5 m were returned to the laboratory and kept overnight in large tanks with running seawater. To determine whether marking and/or handling resulted in mortality, half of each sample from each depth was measured and marked as described below, and the other half measured only. The fish in the 4 treatments were then kept in separate tanks, fed minced mussel *Mytilus edulis* ad libidum and checked each morning for deaths for 4 wk.

Marking in the field: Fish were marked on a large table sited near the water's edge sufficient for 3 people to work side by side. Newly caught fish were carefully taken from the buckets and their total length measured. They were then placed eyed-side down on wet paper towels for marking. Marking consisted of a subcutaneous injection on the blind side, of acrylic paint (Rowney 'Cryla') diluted with 3 parts seawater, using 0.5 mm diameter hypodermic needles. After marking, fish were placed in separate buckets of aerated seawater before release. A fourth person recorded the length and colour of each fish marked. Each fish was marked with a colour specific to its depth of capture and subsequent treatment as described in the next section.

On the first day of capture and marking (Day 1 at Stn A, Day 2 at Stn B), the mark was positioned ventral to the lateral line. Two days after marking (Day 3 at Stn A, Day 4 at Stn B), all unmarked fish caught were given the appropriate colour mark above (dorsal to) the lateral line. Previously marked fish recaptured 2 d after release were given a second mark of a colour appropriate to their depth of capture but above the lateral line. Any marked fish recaptured >2 d after release were remarked with a previously unused colour.

Release procedure. Immediately after all fish had been marked (about 1 to 2 h after low water), approxi-

mately half of the day's catch from each depth was replaced at the depth of capture (0.5 m marked blue or 2.5 m marked yellow) and the remainder ('transplants') was released at the shallower or deeper depth. That is, half of the fish caught at 0.5 m (marked red) were released at 2.5 m and half of the fish caught at 2.5 m (marked green) were released at 0.5 m. Fish were always released at the station where they were caught; there were no transplants between stations.

Recapture methods. Fish were recaptured around the time of low water (± 1.5 h) using the same method as their initial capture, and the stations were revisited at frequent intervals up to 58 d thereafter (see Table 2). After the initial 4 d marking period, once the fish had been inspected for marks, all marked and unmarked fish were released at the capture site.

The nature of the experimental treatments means that recaptured fish can be allocated to 8 categories depending on their depth of initial capture (shallow, S, or deep, D), the depth in which they were replaced or to which they were transplanted (S or D), and their depth of recapture (S or D). Each of the 8 categories was given a unique recapture code to facilitate description of the results. For example, the code SSS indicates that a fish was initially caught at 0.5 m (S) and released and recaptured at the same depth (SS) whereas the code DDS indicates that a fish was initially caught at 2.5 m (D) and released at 2.5 m (D) and subsequently recaptured at 0.5 m (S) (Table 1).

RESULTS

Effects of handling and marking

Five fish died during the course of the mark effect trials, but there was no significant difference in mortality between marked and unmarked fish ($\chi^2 = 0.65$, $p > 0.25$).

Catches

The numbers of fish caught during the investigation are given in Tables 2 & 3. All 2546 fish caught between 1 and 4 August were marked and released.

The length distributions of marked fish were similar between stations at the same depth, but the mean length of fish at 0.5 m was always less than that at 2.5 m (Table 2). The difference in mean lengths at the 2 depths was caused principally by the virtual absence of fish < 45 mm at 2.5 m, although the maximum lengths were similar at both depths. This difference is reflected in the consistently smaller standard errors of the deeper samples.

Table 1. *Pleuronectes platessa*. Codes allocated to recaptured fish. S: shallow, D: deep

Recapture code	Depth of initial capture (m)	Release depth (m)	Recapture depth (m)
SSS	0.5 (S)	0.5 (S)	0.5 (S)
SSD	0.5 (S)	0.5 (S)	2.5 (D)
SDS	0.5 (S)	2.5 (D)	0.5 (S)
SDD	0.5 (S)	2.5 (D)	2.5 (D)
DDD	2.5 (D)	2.5 (D)	2.5 (D)
DDS	2.5 (D)	2.5 (D)	0.5 (S)
DSD	2.5 (D)	0.5 (S)	2.5 (D)
DSS	2.5 (D)	0.5 (S)	0.5 (S)

Recaptures

General recapture statistics

Approximately equal numbers of fish caught over the 58 d of the observations were caught and marked in deep and shallow water (Tables 2 & 3). Of these, 351 were recaptured at least once (Table 3), representing 5.2% of the total catch or 13.8% of the 2546 marked fish.

Recapture rates of marked fish were much greater in shallow water (263; Table 3) than in deep water (88). Twelve fish were recaptured twice, all at 0.5 m. Of these 12 double recaptures, 8 had been transplanted from shallow to deep water and the remaining 4 had been caught and replaced in shallow water. Overall, a much greater percentage of fish initially caught and marked in shallow water (270 of a total of 1274, 21.2%) were recaptured compared with those initially caught and marked in deep water (81 of a total of 1272, 6.4%); (Table 3). To test the hypothesis that the probability of recapture is independent of the depth of initial capture, i.e. fish initially caught in deep water have the same recapture rate as those initially caught in shallow water, a chi-squared test was applied to the contingency table given in Table 4A. The resulting $\chi^2 = 117.7$ was significant at $p \ll 0.0001$, and the null hypothesis was rejected. The depth of release rather than the depth of initial capture could also affect the probability of recapture, and so the following null hypothesis was tested: The probability of recapture is independent of the depth to which the fish were returned after tagging. The contingency table for this test is given in Table 4B. The resulting χ^2 of 0.77 was not significant ($p = 0.380$), and the null hypothesis was accepted.

Fidelity and depth selection

Nearly all of the recaptures of fish that had been caught and released at their original depth of capture (SSS, DDD) were made at that depth, and the propor-

Table 2. *Pleuronectes platessa*. Summary of total catches of fish during the experiment. The means \pm SE of total length (mm) for catches made on Days 1 to 4 are shown in parentheses

Date	Days after marking	Stn A		Stn B		Total
		0.5 m	2.5 m	0.5 m	2.5 m	
1 Aug (Day 1)	0	285 (49.2 \pm 0.6)	370 (60.3 \pm 0.4)	–	–	655
2 Aug (Day 2)	0	–	–	394 (52.4 \pm 0.5)	279 (60.7 \pm 0.4)	673
Total (Days 1, 2)						1328
3 Aug (Day 3)	2	302 (52.1 \pm 0.6)	315 (61.1 \pm 0.4)	–	–	617
4 Aug (Day 4)	2	–	–	293 (56.1 \pm 0.7)	308 (60.5 \pm 0.4)	601
Total (Days 3, 4)						1218
7 Aug	4, 6	268	245	–	–	513
9 Aug	5, 7	–	–	303	242	545
Total						1058
14 Aug	11, 13	404	298	–	–	702
16 Aug	12, 14	–	–	197	264	461
Total						1163
28 Aug	25, 27	343	272	–	–	615
30 Aug	26, 28	–	–	253	257	510
Total						1125
28 Sep	56, 58	202	248	–	–	450
29 Sep	56, 58	–	–	217	195	412
Total						862
Grand total		1804	1748	1657	1545	6754

tions were very similar in deep and shallow water (47.0 and 43.2%, respectively; Table 5, Fig. 1). Very few had voluntarily changed their depth and were subsequently recaptured at other depths (SSD 2.6%, DDS 1.2%; Table 5, Fig. 1). Furthermore, almost all of the recaptures of fish that had been marked and transplanted to another depth were made at the original depth (SDS, DSD) and the proportions were very similar in deep and shallow water (48.5 and 50.6%, respectively; Table 5, Fig. 1). Very few were recaptured at the depth to which they had been transplanted (SDD, DSS) (Table 5, Fig. 1). These results suggest that fish have a strong depth preference, do not move readily from that depth and will return to that depth if displaced. To

test this suggestion, the following null hypothesis was tested: Movement pattern after treatment is independent of the depth of initial capture, i.e. fish caught in, and returned to, shallow water (SS) are just as likely to move into deeper water as fish caught in deep water and released in shallow water (DS), and vice versa. The contingency tables for this hypothesis are given in Table 6. The resulting chi-squared tests were very highly significant ($p < 0.0001$) for fish from both shallow (Table 6A, $\chi^2 = 126.6$) and deep water (Table 6B, $\chi^2 = 139.6$), enabling the null hypothesis to be rejected. However, this fidelity is not absolute because supplementary sampling at depths between 0.5 and 5 m between the dates given in Table 2 caught 11 marked

Table 3. *Pleuronectes platessa*. Summary of total catches, releases and recaptures of marked fish over the 58 d of the experiment

Category	Shallow	Deep	Total	% of marked fish
Catch	3461	3293	6754	–
Marked	1274	1272	2546	–
Releases originating from				
Shallow water	613	661	1274	–
Deep water	630	642	1272	–
Recaptures originating from				
Shallow water	258	12	270	10.6
Deep water	5	76	81	3.2
Marked fish recaptured	263	88	351	13.8

Table 4. *Pleuronectes platessa*. Contingency table used to test the hypotheses that (A) the probability of recapture is independent of the depth of initial capture and (B) the probability of recapture is independent of the depth to which the fish were returned after tagging

	No. recaptured	No. not recaptured	Total
(A) Depth of origin			
Shallow	270	1004	1274
Deep	81	1191	1272
Total	351	2191	2546
(B) Depth of release			
Shallow	179	1064	1243
Deep	172	1131	1303
Total	351	2195	2546

Table 5. *Pleuronectes platessa*. Summary of recaptures of marked fish at intervals during the course of the experiment. Key to the recapture codes is given in Table 1

Days after marking	Fish initially captured in shallow water							Fish initially captured in deep water										
	SSS		SSD		SDS		SDD		Total (n)	DDD		DDS		DSD		DSS		Total (n)
	n	%	n	%	n	%	n	%		n	%	n	%	n	%	n	%	
2	18	37	0	0	31	63	0	0	49	47	7	0	0	47	7	6.7	1	15
4-7	43	49	1	1	42	48	1	1	87	10	43	0	0	13	57	0	0	23
11-14	34	50	2	3	32	47	0	0	68	7	33	0	0	14	67	0	0	21
25-28	22	51	2	5	18	42	1	2	43	7	58	0	0	3	25	2	17	12
56, 58	10	43	2	9	8	35	3	13	23	4	40	1	10	4	40	1	10	10
Totals	127	47.0	7	2.6	131	48.5	5	1.9	270	35	43.2	1	1.2	41	50.6	4	4.9	81

fish (5 SS, 5 SD, 1 DD) at 0.9 m, 8 to 10 d after marking, and 15 (2 SD, 10 DD, 3 DS) at 1 to 2 m, 28 d after marking. Further supplementary sampling at depths of >5 to 11 m and 59 to 99 d after marking caught some marked fish at these depths; a further indication of the offshore movement at this time.

Temporal patterns of recaptures

Marked fish made up 5.3% of the total catch 2 d after marking, and this percentage rose to 10.4 during Days 4 to 7 (Table 7), after which it steadily declined, perhaps indicating a movement of marked fish into deeper water beyond the outermost sampling depth or selective mortality of marked fish. Many transplanted fish (SDS, DSD) had returned to their original depth within 2 d, but the percentage of fish returning to shallow water after transplantation (SDS) showed a decline with time. A similar trend was not obvious in the other

category of transplanted (DSD) fish, although the numbers of recaptures were smaller (Table 5). However, there was a clear temporal trend in the proportions of fish initially caught in shallow water recaptured in deep water (Table 7). To test the null hypothesis that there is no change in the rates of movement of shallow water fish between depths over time, a chi-squared test was applied to the data condensed to <11 and ≥11 d to ensure that expected values were >5 (Table 8). The resulting χ^2 of 5.71 was significant at $p = 0.017$, so the null hypothesis was rejected, a further indication that there was greater movement into, and tendency to remain in, deeper water as the experiment progressed.

Effects of size

Because of the strong relationship between size and depth, it might be expected that there would be a greater tendency for transplanted smaller fish originating from shallow water to return to shallow water than larger fish, and vice versa for fish originating in deep water. In other words, is $L_{SDS} < L_{SDD}$ and $L_{DSD} > L_{DSS}$, where L is mean length? Unfortunately this expectation could not be tested because of the low numbers of

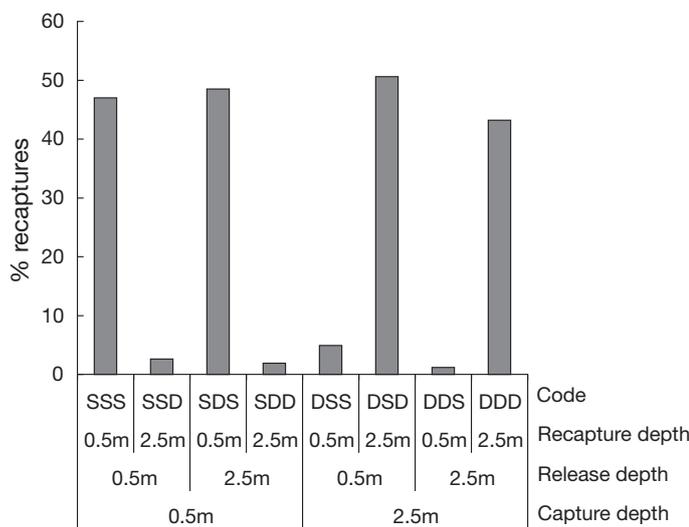


Fig. 1. *Pleuronectes platessa*. Cumulative recaptures over the course of the experiment expressed as a percentage of the 2 treatment types (S: shallow and D: deep), based on data from Table 5. Key to the recapture codes is given in Table 1

Table 6. *Pleuronectes platessa*. Contingency table used to test the hypothesis that movement patterns after treatment are independent of the depth of initial capture. Data from Table 5 and with the recapture codes shown. Key to the recapture codes is given in Table 1

Depth of initial capture	Recapture depth		Total
	Shallow	Deep	
(A) Fish released in shallow water			
Shallow	127 SSS	7 SSD	134
Deep	4 DSS	41 DSD	45
Total	131	48	179
(B) Fish released in deep water			
Deep	1 DDS	35 DDD	36
Shallow	131 SDS	5 SDD	136
Total	132	40	172

Table 7. *Pleuronectes platessa*. Variation in recapture rate of marked fish with time

Days after marking	Total catch (from Table 2)	No. marked fish recaptured (from Table 5)	% marked fish in catch	% shallow water fish recaptured in deep water
2	1218	64	5.3	0
4–7	1058	110	10.4	2.3
11–14	1163	89	7.6	2.9
25–28	1125	55	4.9	7.0
56, 58	862	33	3.8	21.8

fish recaptured at the earliest stages of the experiment. Fish at later stages would have grown and so their original length could not be known, thereby confounding the comparison.

DISCUSSION

Depth is an environmental factor that commonly plays an important part in determining the distribution of numerous aquatic organisms, and many species are restricted to a characteristic depth range over their lifetime. However, motile species may occupy only part of that range at different stages in their development and growth. The underlying implication of differential depth distribution between sizes, developmental or reproductive stages is that individuals can detect, select and maintain their position at particular depth or within a range of depths.

Flatfishes provide many examples of differences in depth distribution within and between species (e.g. Gibson 1973, Riley et al. 1981, Macpherson & Duarte 1991, Allen & Balz 1997, Armstrong 1997), but the studies are mainly descriptive and the extent to which such distributions are the result of external factors or of active choice has not been widely investigated. The results given in this paper provide clear evidence that individual young plaice on their nursery ground show

Table 8. *Pleuronectes platessa*. Contingency table used to test the null hypothesis that there is no change in the rates of movement of shallow water fish between depths over time. Data from Table 5 with recapture codes shown. The key to the recapture codes is given in Table 1

Days after marking	Recapture depth		Total
	Shallow SSS + SDS	Deep SSD + SDD	
<11	134	2	136
≥11	124	10	134
Total	258	12	270

little short-term variation in the depth occupied, indicating they can actively maintain their position at a given depth. Furthermore, the experiments demonstrated that transplanted individuals do not remain at the transplant depth and rapidly return to their original depth, thereby providing further evidence for active depth selection. This 'homing' to the depth formerly occupied can be rapid, within 2 d and probably even less, although the initial sampling frequency did not allow a

more accurate measure. Return within 1 tidal cycle would certainly be possible because the return journey would have been ~100 m, a distance that the fish cover 4 times a day in the course of their intertidal migrations on the beach used for the experiments. Depth fidelity is also largely maintained as the fish undergo their intertidal movements (Gibson 1973), at least during the day, although there is a marked tendency for the population to be shallower at night (Gibson et al. 1996, Burrows 2001).

This fidelity to a particular depth can be compared with the horizontal site fidelity shown by young winter flounder *Pseudopleuronectes americanus* (Saucerman & Deegan 1991) and plaice (Riley 1973, Burrows et al. 2004), in which individuals do not stray far alongshore. Juvenile plaice also show 'homing' whereby they return to their original position when laterally displaced (Riley 1973, Burrows et al. 2004) and on a larger scale, the ability of the adults to return to spawning and feeding grounds is well documented (e.g. Hunter et al. 2003, Solmundsson et al. 2005). The clear depth fidelity of young plaice and the overall phenomenon of differential depth distribution poses the intriguing question of how it comes about.

In a review of this relationship in fishes, Macpherson & Duarte (1991) concluded that, where present, it derives from migratory or diffusive movements from shallow to deep water during ontogeny following the initial onshore drift and/or migration of larvae and the subsequent occupation of shallow water by juveniles (p. 109 in their paper). The life history of plaice (see 'Introduction') agrees well with this conclusion. Small juvenile plaice are restricted to shallow depths, whereas larger ones cover the entire juvenile depth range (Gibson et al. 2002), a 'smaller–shallower' mechanism (Middleton & Musick 1986) rather than simply 'bigger–deeper': a trend of increasing mean size with depth (Polloni et al. 1979). In relation to the importance of temperature gradients in determining distribution, Macpherson & Duarte (1991, p. 110) also commented that size–depth relationships occur over a much narrower depth range in fresh water where significant

temperature gradients are often present within a few metres depth. A similar situation occurs in the shallow marine waters that young plaice inhabit (see e.g. van der Veer & Bergman 1986, Gibson et al. 2002). Over a wider scale to encompass the whole depth distribution of a species, Macpherson & Duarte (1991) further concluded that fish move into deeper water as they grow in order to benefit from a lower metabolism and extended life span at lower temperatures and suggest that the pattern is evolutionary in nature and has a genetic basis.

For the few months during and after settlement, the choice of depth and the length–depth relationship in young plaice undergoes several changes, implying that the preferred depth changes accordingly. In the first phase, represented by the onshore movement of metamorphosing larvae, individuals appear to settle offshore and then move inshore to congregate in the shallowest water possible, often a few centimetres deep, as though constrained only by the waterline. At this stage in the process, the first settlers have had time to grow and so are larger than later, smaller settlers still moving onshore. The length–depth relationship at this time is therefore negative. Once settlement is completed, the population goes through a brief period when there is no relationship between length and depth. The cause of this change is not known; it may be due to a movement of the larger fish in the population into slightly deeper water, i.e. a change in depth preference as size increases, or by faster growth of those fish at the deeper end of the distribution, or both. Whatever the cause, the change eventually results in a strong positive length–depth relationship that remains stable for several weeks. At the start of this period, individuals seem to have acquired a preference for (or perhaps begin to express an inherited tendency to select) a specific depth because the fish do not adjust their depth as they grow. Such a depth adjustment would be expected if there was a fixed relationship between length and depth, i.e. fish of a particular size are always found at a characteristic depth. Statistically, this phenomenon is represented by an increase in the intercept of the regression line describing the length–depth relationship whereas the slope remains constant (Gibson 1973, Gibson et al. 2002). It was towards the end of this stable period that the experiments described in this paper were done, and the results provide evidence to support the suggestion that individuals have a preference for a set depth. Following the stable period, a third change takes place and there is general movement offshore indicating a further change in preferred depth. Eventually, the great majority of fish emigrate to deeper water. This offshore movement was also detected during the later stages of the experiment.

A further question raised is how to reconcile the presence of contrasting patterns of depth choice with our current understanding of the evolutionary selective pressures influencing behaviour. Burrows (1994) constructed models of depth selection behaviour in young plaice based on the premise that fish adopt depths through tidal and diel cycles that give the best balance between finding food and avoiding predators. The strong fidelity for a specific depth that varied among individual fishes shown in the present study conflicts with this premise, and suggests that depth preference may be much less dynamic over tidal and diel cycles than previously thought.

The weak association between depth fidelity and fish size was surprising. Similar-sized and outwardly identical fishes had contrasting depth preferences, although the smallest fish were always absent from deeper water. Optimality models for habitat choice (Clark & Levy 1988, Burrows 1994) never predict 2 solutions to the same trade-off problems, making explanations for depth choice as selective advantages or trade-offs very difficult.

Varying strong preferences for depth in otherwise similar fishes suggest internal control mechanisms. Persistent differences in behaviour and physiology among individuals are sometimes termed behavioural syndromes (Sih et al. 2004) or 'personality traits' (Stamps 2007). We have no evidence as to whether observed depth preferences in young plaice have a phenotypic or genotypic basis, but it is possible that such differences may arise as a result of different experiences during early life (Davis & Stamps 2004). Post-larval plaice settling on sandy beaches may have had varying durations of planktonic development, and successful settlement of early-arriving larvae may require a faster growth rate than for late-arriving larvae. Different physical conditions through larval development may also have affected subsequent growth rate (Hovenkamp 1992, van der Veer et al. 2000).

If depth preferences have a genetic element, the different behavioural strategies adopted may represent evolutionary bet-hedging (Philippi & Seger 1989). Preference for shallow water may be a superior strategy in nursery areas where food resources are richer and predators rarer in shallow water, while deep-water preference may be a more successful strategy where predators are rarer and food is more plentiful at depth.

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