Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground

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ABSTRACT: Stratified depth sampling was used to investigate the distributional changes of newly settled plaice *Pleuronectes platessa* and dabs *Limanda limanda*, and resident populations of shrimp *Crangon crangon* on a sandy beach. During the settlement period, the smallest newly settled plaice are found in deeper water than the larger fish that settled earlier. After settlement, plaice concentrate in water <1 m deep and there is a positive relationship between length and depth. Later in the year the fish gradually migrate into deeper water as they grow. Dabs settle later and in deeper water than plaice. Shrimp are concentrated in deeper water early in the year but migrate onshore in the summer. The movements of plaice are considered to be related to the predation risk caused by the shrimp and other predators in deeper water and to the higher temperatures in shallow water that promote faster growth. Once a size refuge from predators has been reached, the plaice move into deeper water. Intertidal pools probably serve as refuges for the smallest sizes of plaice because predators are less numerous in pools than in the sea. The use of shallow water by plaice represents the occupation of a niche which not only reduces predation and maximises growth, but may also greatly reduce competition for food in the earliest stages when densities are highest and competition with dabs is likely to be greatest.

KEY WORDS: Depth distribution · Predation · Competition · Growth · Sandy Beaches · Migration · Plaice · Dab · Shrimp

INTRODUCTION

The habitat an animal occupies at any one time is the result of a complex series of responses to environmental factors such as availability of food and shelter, predation risk and physicochemical conditions. Some factors may act in opposition so that the actual habitat occupied may be a compromise that represents the best balance between them (Huntingford 1993, Burrows 1994, Hughie & Dill 1994, Kramer et al. 1997). In addition, a habitat that is suitable at one stage in the life history may be unsuitable at another, resulting in the differential distribution

of the various developmental stages (Polis 1984). The young stages, for example, are particularly vulnerable to predators and extremes of environmental conditions and are often concentrated in 'nursery' areas. In such areas, the trade-off between growth and survival is optimised because predators are few, food is abundant and the environment is relatively benign. Such a generalisation is probably also true for some early life stages of numerous species of coastal marine fishes that use estuaries and bays for this purpose. Many such species spawn offshore and the routes and mechanisms of larval transport to the inshore nursery grounds are of considerable interest (Boehlert & Mundy 1988, Forward & Tankersley 2001). Metamorphosis from the larval to the juvenile stage, and for benthic species settlement onto the sea

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bed, usually takes place at or very near to the coast. Settlement processes have been studied most intensively in coral reef fishes (Victor 1991, Öhman et al. 1998) and to a lesser extent in flatfishes (Pleuronectiformes). In the latter group, settlement areas and subsequent nursery grounds are frequently (Bregneballe 1961, Lockwood 1974, Toole 1980, van der Veer & Bergman 1986, Kramer 1991, Subiyanto et al. 1993, Allen & Baltz 1997), but not always (Walsh 1991, Bolle et al. 1994), situated in very shallow water (see Gibson 1994 for review).

Because of its abundance and economic importance, the plaice *Pleuronectes platessa* has received considerable attention in this respect. Previous studies have indicated that it may have 2 settlement strategies that depend on local environmental conditions. In areas that are sheltered from the open sea, as in the Wadden Sea on the Dutch and German coasts, the metamorphosing individuals settle in spring directly into intertidal pools on sandflats, where they remain to feed and grow until environmental temperatures become too high (Berghahn 1983, 1987, van der Veer & Bergman 1986). Subsequently, the juveniles leave the pools but return to the tidal flats with each high tide. On more exposed coasts, the fish appear to settle deeper and then move onshore into very shallow water (Gibson 1973, Lockwood 1974), where intertidal pools, if present, may be occupied temporarily (Cole & Johnston 1901, Berghahn 1987). After this onshore movement, the juveniles' depth distribution remains stable but is further modified in summer by a movement into deeper water (Gibson 1973, Lockwood 1974, Kuipers 1977, Gibson et al. 1996).
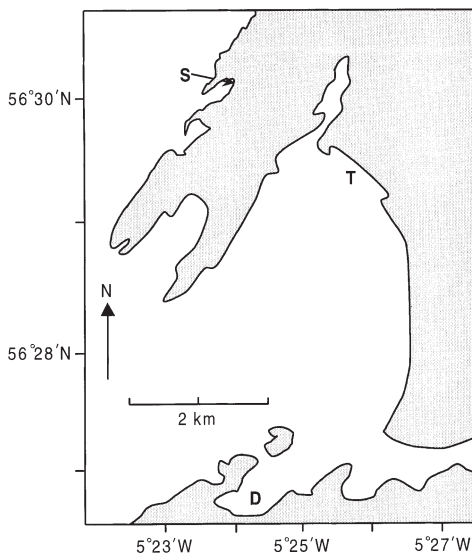

Fig. 1. General location of the study area on the west coast of Scotland. The 3 beaches on which the fieldwork was carried out were Shenavallie (S), Tralee beach (T) and Dunstaffnage Bay (D)

The dab *Limanda limanda* has a very similar general ecology to the plaice, the main difference being that it has a much wider depth distribution in its early juvenile stages (Riley et al. 1981, Bolle et al. 1994). It is very rarely caught intertidally and young-of-the-year dabs overlap spatially with 0-group plaice only at the shallow limit of their distribution. The species thus provides an interesting contrast to the plaice in terms of the factors controlling its distribution.

This paper reports on a detailed examination of the changing patterns of depth distribution of juvenile plaice and dab on a relatively exposed sandy beach from settlement in the spring to the beginning of their offshore movement in the summer. The major objective was to determine whether observed depth distributions could be interpreted in the light of possible gradients of predation risk and temperature. A secondary objective was to determine whether intertidal pools served as refuges from predation for small juvenile flatfishes.

MATERIALS AND METHODS

Sampling sites. All sampling sites were situated within 10 km of each other in the Firth of Lorne on the west coast of Scotland (Fig. 1). The trawl samples were taken on Tralee beach in Ardmucknish Bay. This beach was the site of several previous studies (Gibson 1973, Gibson et al. 1993, 1996, Burrows et al. 1994), and it is described in detail in those publications. Briefly, the beach is sandy, approximately 1 km long, and faces southwest into the prevailing winds. The fish fauna is well known (Gibson et al. 1993), and the area serves as a nursery ground for numerous species, particularly flatfishes. Intertidal pools are rare and transient on Tralee beach, and sampling of natural and artificial pools was carried out elsewhere. The natural pools sampled were situated on a smaller, more sheltered beach at Shenavallie approximately 2 km northwest of Tralee beach. The artificial pools were dug in Dunstaffnage Bay, which lies about 5 km south of Tralee beach. It faces northeast and is therefore sheltered from prevailing winds but has no naturally occurring intertidal pools. Both Shenavallie beach and Dunstaffnage Bay have fish faunas that are very similar to that of Tralee Bay (R.N.G. pers. obs.).

Sampling methods. Samples were taken in 1995, 1996 and 1997 with a 1.5 m beam trawl with a weighted footrope and a single, spiked tickler chain. The mesh of the main part of the net was 8 mm (stretched) and the cod end was lined with 3 mm mesh. In the early months of the last year of sampling (1997), the whole net consisted of 3 mm mesh. The net was towed parallel to the shore line for 5 min in depths of

5, 4, 3, 2, and 1 m by boat, and in 0.5 m by 2 people on foot. The boat was kept at the selected depth during towing by continuous sounding with a graduated lead line. Previous experience (Gibson 1973, Gibson et al. 1996) had shown that the great majority of the 0-group plaice population was contained within these depths during the spring and summer. The distance trawled was measured with a calibrated odometer attached to the frame of the net. The average distance trawled for each sample was approximately 200 m. In 1997 the track of the boat was also plotted using a GPS system. Temperatures at different depths were recorded in 1995 with a 'Tinytalk' temperature logger (RS Components) attached to the trawl frame. In 1996 and 1997 the Tinytalk logger was replaced with a 'Vemco Minilog' depth and temperature recorder (Hydrosphere UK) set at a sampling interval of 5 s. Both recorders have an accuracy of less than ± 0.2°C over the temperature range encountered. The output from the depth recorder was used to calculate the mean depth at which each sample was taken. These mean depths differed from the target depths by an average of 2% in 5 m to 10% in 0.5 m. In August and November 1995, parallel trawls were also made over an equivalent distance with a 3 m beam trawl from a larger boat in depths from 5 to 20 m. These trawls were made to examine the distribution of fish in water deeper than 5 m.

Sampling took place over the low-tide period of daytime spring tides from late March and continued approximately fortnightly, weather permitting, until November each year. All catches were separated from large quantities of weed, where present, in the field. Animals were then anaesthetised in benzocaine (approx 1:25 000) and preserved in approximately 6% formalin.

To study the use of intertidal pools by small fishes, 2 approaches were adopted. In the first, artificial pools were dug on a beach (Dunstaffnage Bay) where they were naturally absent. In the second, fish were sampled inside and outside natural pools on Shenavallie beach. The artificial pools were dug by hand at low tide. Six sites were randomly chosen on a strip of beach 40 m wide at each of 3 levels; 0.8 m above chart datum (CD), i.e. approximately mean low-water spring tides (MLWS); 1.4 m above CD, approximately midway between MLWS and mean low-water neap tides; and 2.15 m above CD, just below mean tide level (2.35 m above CD). Each pool measured 1.4 × 1.4 m with an average depth of 9 to 10 cm, and excavation was completed 5 tidal cycles before sampling began on the ebb tide on 17 May 1995.

Six random 1 m² drop-trap samples (Wennhage et al. 1997) were taken outside the upper pools when the water depth was 0.4 m and the upper pools themselves were sampled as soon as they became exposed. This procedure was repeated for the middle and lower levels as the tide receded. At the time of low water, 6 further random drop-trap samples were taken at a depth of 0.4 m below low-water mark. Water depths were measured during sampling and water temperatures in the pools were recorded 0.5 h after low water. One large natural pool at approximately mean tide level was sampled at Shenavallie beach on 20 May 1995 using a similar procedure: 8 drop-trap samples were taken outside the pool, 14 inside the pool and 12 below low-water mark at low tide.

Laboratory methods. In the laboratory, the catch from each sample was identified and counted, and the total length of all fishes was measured to the nearest millimetre. The 2 major crustacean predators of small fishes, the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas* (Ansell et al. 1999) were also counted and measured. The dimensions measured were total length for shrimp and carapace width for crabs. Shrimp <30 mm from the trawl catches were not included because they are not considered to be a major predatory threat to small fishes (van der Veer & Bergmann 1987, Gibson et al. 1995). The distribution and abundance of shore crabs were not analysed further because the sample sizes were too small to provide meaningful results.

Data analysis. All trawl catches were standardised to numbers of individuals per 100 m² trawled and not corrected for net efficiency. The median depths of plaice, dabs and shrimp were calculated for all dates on which a complete set of depth samples (0.5 to 5 m) was obtained. A linear regression of length on depth was also calculated for each date using Microsoft Excel. Frequencies of size classes of plaice, dab and shrimp at each depth were summed over all sample dates in each year to calculate averages and standard deviations of depth for each size class. The small number of shore crabs caught in the trawl samples prevented any further meaningful analysis for this species.

The lengths and abundances of plaice and shrimp in each drop-trap sample inside and outside pools at each level were subjected to within-species comparisons using the Kruskal-Wallis test (Zar 1996) followed by a multiple comparison of the results.

RESULTS

Variation in water temperature with depth and season

Water temperatures were 6 to 8°C in March and increased steadily to their maximum (approximately 14°C) in late August to mid-September (Fig. 2a). From April to September, temperatures at the shallowest depths sampled (0.5 and 1 m) were consistently higher
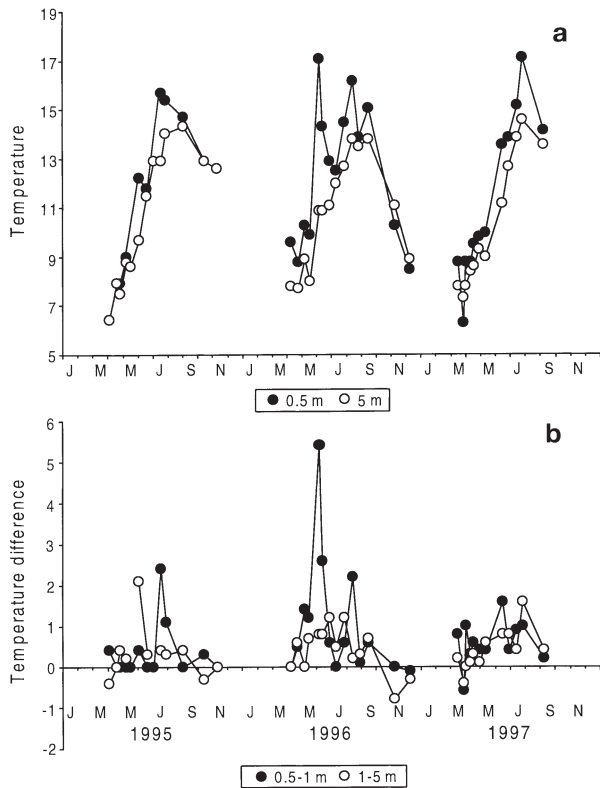
Fig. 2. (a) Temperatures (°C) at 0.5 and 5 m depth at Tralee beach over the study period; (b) temperature differences (°C), between 0.5 and 1 m and 1 and 5 m at Tralee beach

than those at 5 m and sometimes substantially higher than those at intermediate depths as well (Fig. 2b). In March and October to December, this gradient was reversed or absent, and temperatures in shallow water were usually the same as, or less than, those at greater depths (Fig. 2b).

Species composition of trawl catches

As in previous studies (Gibson 1973, Gibson et al. 1993), the benthic fish fauna was dominated by juvenile plaice and dabs whose abundance varied seasonally and between years (Fig. 3). Brown shrimp (Fig. 3) and shore crabs were the dominant large crustaceans.

Changes in median depth with time

Plaice

From the beginning of the settlement season in early April until the end of June, the great majority of fish were caught in depths of 1 m or less. This pattern was consistent in all 3 years (Fig. 4). Once settlement was

complete (late May to June), large numbers (often >70% of the total catch) were caught in 0.5 m, suggesting that the fish were concentrating at this depth. From the end of June, the median depth of the sampled population steadily increased until in October it was >2 m. From April to June the median is a reasonably accurate measure of the centre of the population distribution, because only a small percentage of the total catch was found in depths of >4 m. Later in the year, however, the calculated median depths are underestimates because samples were only routinely taken to 5 m. Additional samples taken at depths >5 m showed that fish were present there also.

Dabs

Dabs were much less abundant than plaice in all years (Fig. 3) but were caught in all the depths sampled. They were usually more or less equally distributed over all
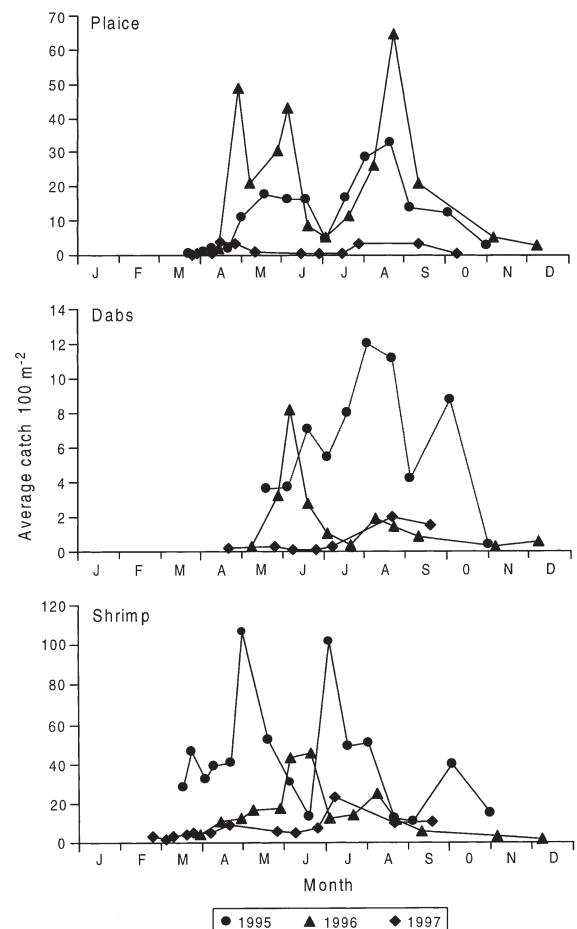

Fig. 3. *Pleuronectes platessa*, *Limanda limanda* and *Crangon crangon*. Seasonal and annual variation in the average catch per 100 m² trawled at Tralee beach in 1995, 1996 and 1997

depths to >5 m and the calculated median depth fluctuated greatly between dates with no clear pattern (Fig. 4). The generally small catches may have contributed to these apparent fluctuations. Dabs settle over a much wider depth range than plaice, and so the data only represents the inner limit of their depth distribution.

Shrimp

The pattern of change in the depth distribution of the sampled population of shrimp was opposite to that observed for plaice. Early in the year the median depth was generally >1 m, but then gradually decreased until late July after which it stabilised between 0.5 and 1 m (Fig. 4). For this species the median is a realistic estimate of the centre of distribution of the population because shrimp were rare at depths >5 m.

Changes in mean length with depth and time

Plaice

The relationship between mean fish length and depth changed throughout the season. During the main settlement period in April and May, the smallest fish were found predominantly in deeper water and the regression of length on depth was either negative or not significantly different ($p > 0.05$) from zero (Fig. 5). By mid-June, the fish were longer and this relationship had reversed so that the mean length of fish increased with increasing depth (Fig. 5b,c). From late June onwards the positive relationship was caused principally by the absence of small fish in deeper water (Fig. 5 c) and was maintained until the end of the year, although the slope of the regressions declined from June onwards (Fig. 6). This seasonal pattern of change in the length-depth relationship was consistent between years (Fig. 6).

Dabs

Over the depth range sampled, the seasonal pattern of change in the length/depth distribution of dabs was similar in outline to that of the plaice. Newly settled fish first appeared in the samples in early to mid-May but were not common until June. In this early part of the settlement season the length-on-depth regressions were either non-significant or significantly positive (Fig. 6). In July and August the relationship was strongly and significantly positive in all 3 yr for which data were available. In most subsequent samples the regressions were not significant. The switch in the
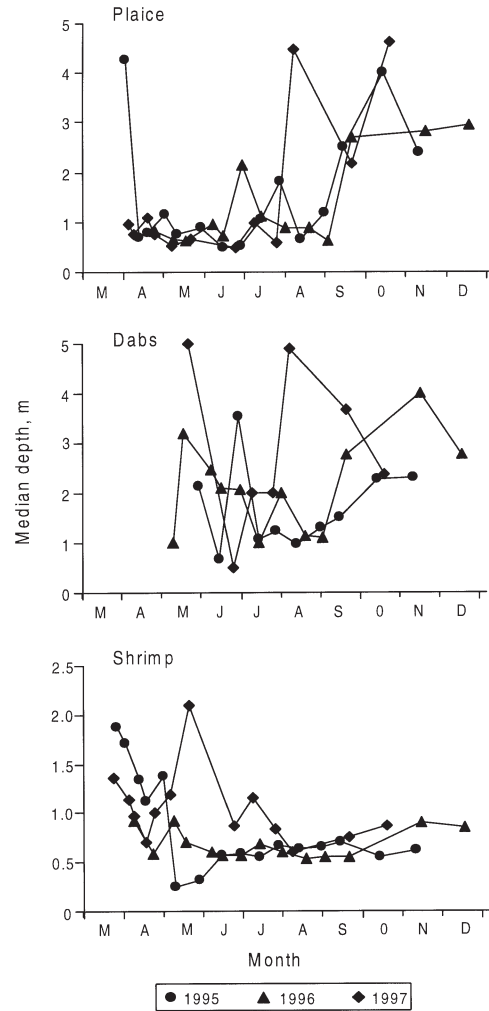

Fig. 4. *Pleuronectes platessa*, *Limanda limanda* and *Crangon crangon.* Median depths of plaice, dabs and shrimp trawled at Tralee beach in 1995, 1996 and 1997
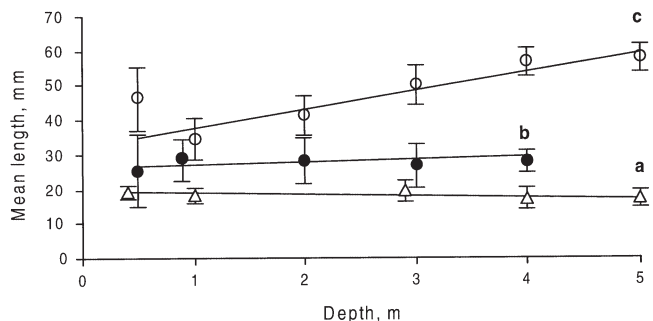

Fig. 5. *Pleuronectes platessa.* Length vs depth relationships at Tralee beach on (a) 8 May 1996, (b) 6 June 1996 and (c) 28 June 1996. Means ±1 SD are plotted with a fitted least-squares regression line for all data on each date. The outlier at 0.5 m on 28 June (c) is probably due to the small sample size (n = 6). Significances for the 3 regressions (a) are $p < 0.0001$, (b) $p = 0.017$ and (c) $p < 0.0001$
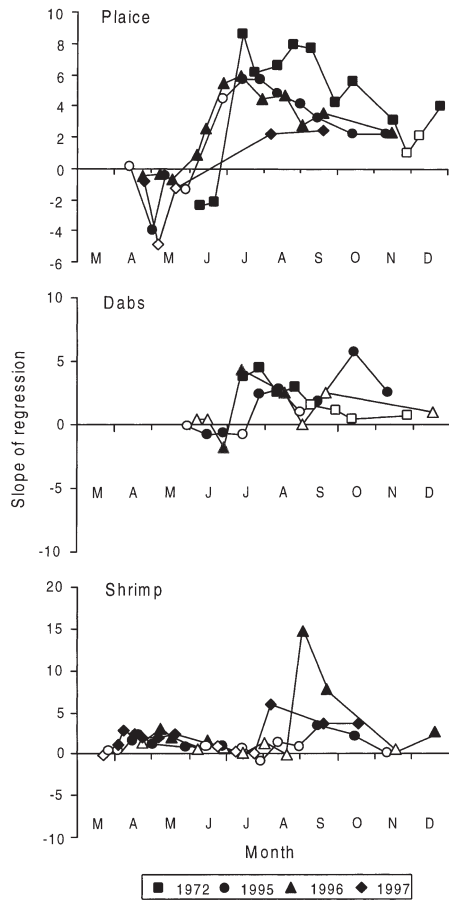
Fig. 6. *Pleuronectes platessa*, *Limanda limanda* and *Crangon crangon.* Seasonal and annual differences in the length (mm) on depth (m) regressions in 1995, 1996 and 1997. Data for plaice and dabs in 1972 are based on Gibson (1973). Non-significant ($p > 0.05$) regressions are indicated by open symbols. Fewer results were available in 1997 because of the low abundance of fishes in that year

relationship from negative or non-significant to strongly positive occurred about a month later than in plaice, reflecting the later settlement of the dabs.

Shrimp

In contrast to the flatfishes, the length/depth distribution of shrimp showed weaker and opposite seasonal changes. From March to May the length-on-depth regressions were mostly significant and positive, whereas in June and July they were non-significant (Fig. 6). After July the situation varied between years, although many regressions again became positive. The large positive values for regression coefficients at this time were caused by the concentration of individuals in shallow water.

Mean depth as a function of size

The pattern of size distributions with depth could be due to ontogenetic, size-related changes in behavioural depth preference. Changes in mean depth for a given size were examined for evidence to test this hypothesis for plaice, dab and shrimp. The patterns for plaice and shrimp were consistent between years (Fig. 7).

Plaice

Plaice between 30 and 50 mm were found in the shallowest water, while plaice < 20 mm were found in slightly deeper water. The depths at which plaice > 50 mm were found increased linearly with size, such that the largest fishes were found on average in the deepest water. Plaice of a given size were caught in deeper water in 1996 than in 1995 or 1997. Plaice 30 mm long had an average depth of 0.5 to 0.6 m in 1995 and 1997, but were found on average at 1.0 to 1.5 m in 1996.

Dabs

In 1995 dabs showed a similar J-shaped distribution with depth to plaice (Fig. 7). When dabs < 30 mm were found in 1995 and 1997, they tended to be in deeper water around 2 m depth than the 30 to 50 mm fish found at about 1 m depth. Dabs > 50 mm were found in increasingly deep water, such that individuals > 80 mm were found only at the deepest depths sampled in 1995. The small sample sizes obtained in 1996 and 1997 preclude any firm conclusions, but in 1996 the positive trend of size with depth for fish > 30 mm resembles that in 1995. The changes in mean depth with size in 1995 and 1996 were not seen in 1997.

Shrimp

In contrast to the fish species, shrimp showed no change in mean depth with size in any of the 3 years of observations (Fig. 7).

Occupation of intertidal pools

Three species were commonly captured in the pools dug on the beach in Dunstaffnage Bay: 0-group plaice, brown shrimp and shore crabs. Occasional small individuals of the short-spined sea scorpion *Myoxocephalus scorpius* were also encountered at the lower levels. No dabs were seen in any pools. Plaice were more abundant in the lower pools than in the mid-level pools ($p < 0.02$,

Fig. 8) and absent from the upper pools. Shrimp showed a similar decrease in numbers in the pools with increase in shore level (p < 0.005, Fig. 8). Plaice and shrimp were only significantly more abundant (p < 0.005, Fig. 8) in pools than outside them at the lowest level.

The lengths of plaice ranged from 15 to 38 mm and were similar in all samples (p > 0.20, Fig. 9). Shrimp (range 23 to 53 mm) were significantly longer in the highest pools than in those at lower levels (p = 0.003, Fig. 9). There was no significant difference in lengths at different shore levels outside the pools (p < 0.05).

At Shenavallie, plaice were significantly lower in abundance (p = 0.03) outside the pools (Fig. 10) than at the other 2 locations, but there was no significant difference in abundance of shrimp (p = 0.07) among the 3 locations. Plaice caught at low water were significantly smaller than those caught higher up the beach (p < 0.002, Fig. 10), whereas shrimp were significantly larger in the samples taken at low water (p < 0.001, Fig. 10).

As an indication of the relative risks of predation in pools and in the area below low water, the shrimp/plaice ratio was calculated for the pools and the area below water at both locations. Only shrimp > 30 mm and plaice < 30 mm were taken into account, based on the critical sizes given by van der Veer & Bergmann (1987).

At Dunstaffnage, plaice were absent from the upper pools, but the proportions of shrimp to plaice were not significantly different in the pools at the 2 lower levels (χ^2 test, p > 0.05) and the 2 sets of data were combined. The combined data gave a predator:prey ratio of 0.37 (Table 1). The equivalent value for samples taken below low water (5.25) was significantly higher than the proportion of predators to prey found in the pools. The shrimp:plaice ratio in the Shenavallie pool was
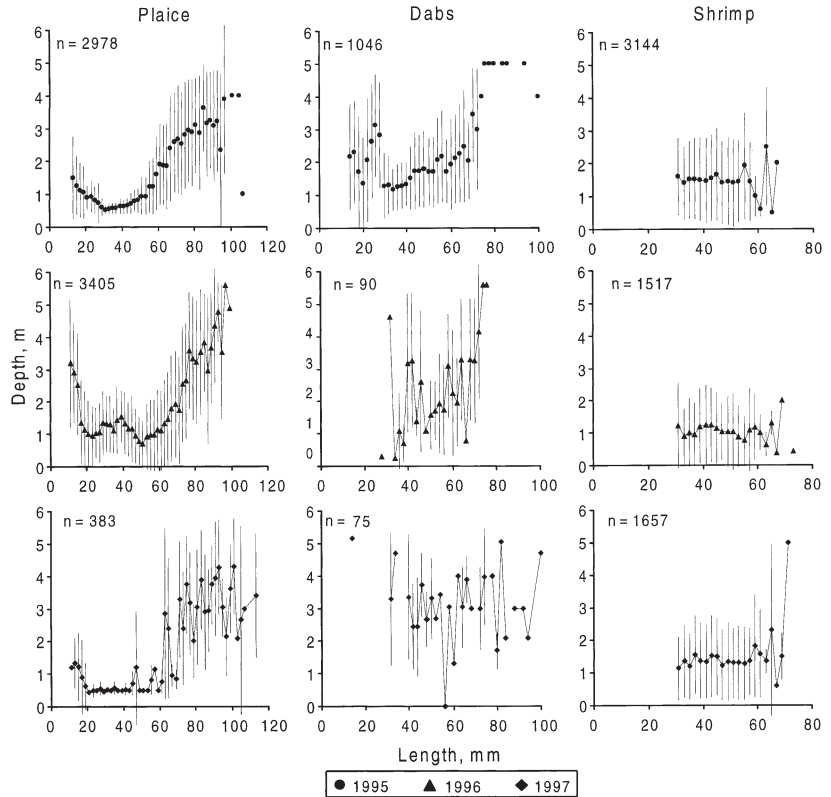

Fig. 7. *Pleuronectes platessa*, *Limanda limanda* and *Crangon crangon.* Mean (±1 SD) depth as a function of size class at Tralee beach in 1995 (top), 1996 (middle) and 1997 (bottom)

similar (0.42: Table 1) to that in the Dunstaffnage pools, but the ratio for the area below low water was much lower (0.85) than at Dunstaffnage. Nevertheless, the 2 proportions at Shenavallie were also significantly different.

DISCUSSION

The principal aim of the work described in this paper was to determine whether observed patterns of distribution of 0-group plaice could be related to possible gradients of water temperature and predation risk. The

Table 1. *Pleuronectes platessa* and *Crangon crangon.* Comparison of predator:prey ratios (shrimp:plaice) in pools and below low-water mark at 2 locations. Probability values are given for the comparison of proportions in pools and below low-water mark using the χ^2 test with 1 df

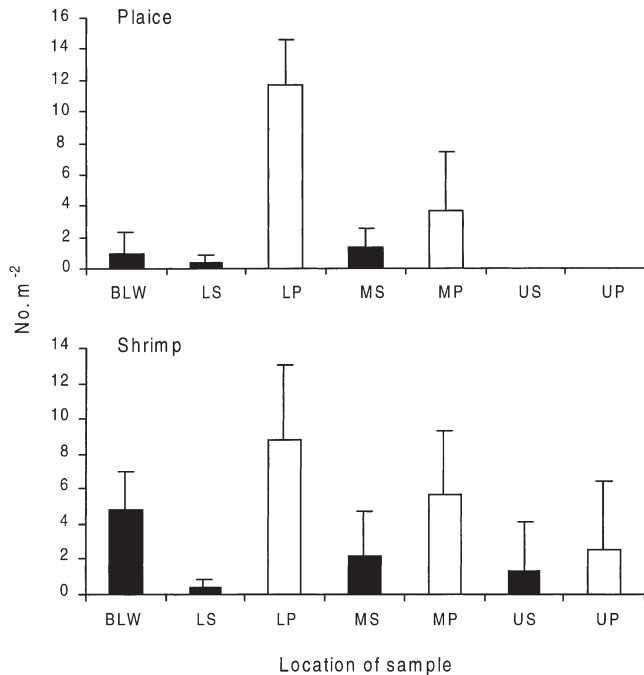| Location	Numbers in pools			Numbers below low water			p
	Shrimp (S)	Plaice (P)	S:P ratio	Shrimp (S)	Plaice (P)	S:P ratio	
Dunstaffnage	34	92	0.37	21	4	5.25	<0.001
Shenavallie	25	59	0.42	46	54	0.85	<0.025

Fig. 8. *Pleuronectes platessa* and *Crangon crangon.* Mean (+1 SD) abundances inside and outside intertidal pools in Dunstaffnage Bay at the following locations: below low water mark (BLW), outside lower pools (LS), inside lower pools (LP), outside mid pools (MS), inside mid pools (MP), outside upper pools (US) and inside upper pools (UP). In-pool samples are shown as open bars
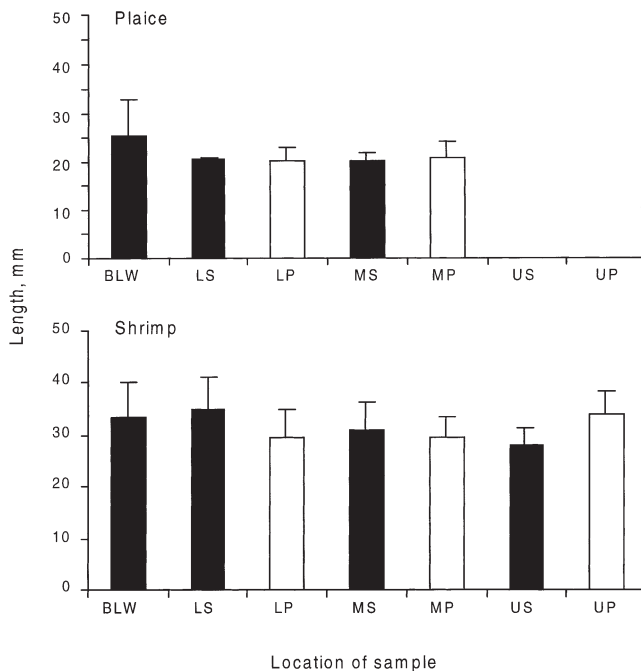

Fig. 9. *Pleuronectes platessa* and *Crangon crangon.* Mean (+1 SD) lengths inside and outside intertidal pools in Dunstaffnage Bay. Abbreviations as in Fig. 8

observations made over 3 years consistently showed that plaice are concentrated in very shallow water (<1 m) for several weeks after settlement, thereby confirming earlier findings at the study site (Gibson 1973, Gibson et al. 1996) and elsewhere in the species' range (Kuipers 1973, Lockwood 1974, Riley et al. 1981). The depth of settlement was not determined exactly because, except in the first samples in 1995, few newly settled individuals (<15 mm) were captured. This absence of newly settled fish in the catches may be an artefact of the gear used (although the 3 mm lining of the trawl cod-end should have retained at least some fish of this size if they were present) or it may indicate that metamorphosing fish settle at depths >5 m. Further circumstantial evidence for settlement at >5 m is the negative length-depth relationship observed during the settlement season. This negative length-depth relationship is interpreted as a result of settlement at >5 m followed by an onshore movement of settled individuals, as described by Lockwood (1974) for the east coast of England. An alternative explanation could be that fish settle at all depths up to the water's edge, but those settling in deeper water suffer higher predation rates and are rapidly replaced by small new settlers. In the shallows, more fish survive and grow, resulting in higher mean lengths in shallower water. Whatever the depth range over which fish settle, once settlement is complete the majority of the year class is concentrated in depths <1 m.

Concentration of juvenile stages in shallow water, positive relationships between body size and depth, and ontogenetic habitat shifts are common phenomena in shallow marine ecosystems (e.g. Ruiz et al. 1993, Macpherson 1998) and have been described in several species of flatfishes (e.g. Gibson 1973, Toole 1980, Riley et al. 1981, Subiyanto et al. 1993, Allen & Baltz 1997, Armstrong 1997). It is likely, therefore, that if these distributions are the result of active selection processes, they confer strong selective advantages upon the individuals that show them. The young stages of all species are subject to high mortality, predators are known to affect prey distributions (Power 1987), and reduction of predation risk is one advantage considered to accrue from living in shallow water (Ruiz et al. 1993). Furthermore, both field observations (van der Veer & Bergman 1987, Ellis & Gibson 1995) and laboratory experiments (van der Veer & Bergman 1987, Gibson et al. 1995, Ellis & Gibson 1997, Wennhage 2000) have demonstrated that predation on young plaice and other flatfishes (Witting & Able 1993) is size-dependent. In addition, those fishes known to prey on young plaice (Ellis & Gibson 1995, Gibson & Robb 1996) are more common in deeper water (Gibson et al. 1996). Consequently, the concentration of small newly settled fish in depths of <1 m should maximise

their probability of survival. Before the end of May and mid-June the greatest density of one of their invertebrate predators, brown shrimp, is in somewhat deeper water (Fig. 4), so that overlap between them is minimised. After this period the onshore migration of shrimp (Boddeke 1976 and present Fig. 4) takes place, but by this time most of the plaice population has grown to a length at which they are less vulnerable to shrimp predation. The time at which plaice settle may, however, be critical. In shallow Swedish bays the early settlers survive best (Modin & Pihl 1994), whereas on the coast of Wales early settlers suffered much higher mortalities than those cohorts settling later in the season (Al-Hossaini et al. 1989). These differences in mortality rates are most probably due to differences in predation rates. In Swedish bays, plaice tend to settle, grow, and obtain a refuge in size before the main immigration of shrimp. Modelling studies taking into account the predator-prey size relationship between plaice and shrimp (van der Veer & Bergman 1987, Gibson et al. 1995) predict that if shrimp arrive early or overwinter on the nursery grounds and are large, then plaice survival will be lower than if the shrimp arrive later and are smaller (Burrows et al. 2001). Such effects could give rise to a latitudinal gradient in the impact of crustacean predation (van der Veer et al. 1990), because it can be hypothesised that this impact would increase towards the southern end of the species range.

Living in shallow depths also means that the plaice avoid to a large extent predation by another of their invertebrate predators, the shore crab, which Ansell et al. (1999) consider could have a predatory impact 30 times greater than that of shrimp. Shore crabs are most abundant at depths of >2 m during the day, although they are shallower and more abundant at night (Ansell et al. 1999). Overlap between this predator and the smallest plaice is therefore low, and any diel changes in the distribution of crabs is matched by those of the plaice (Burrows et al. 1994, Gibson et al. 1998).

Occupation of intertidal pools is also likely to reduce predation mortality. Although some predation probably occurs in these pools, the field observations described in this paper (Table 1) show that predator:prey ratios are significantly lower inside than outside pools. Encounter and hence capture rates in pools are thus likely to be reduced compared with the situation elsewhere. Furthermore, residence in pools over the low-water period means that the fish are isolated from the predators in deeper water for a significant part of the tidal cycle, and there appears to be no published evidence for significant predation by birds at low tide. It is probably no coincidence, therefore, that the major nursery grounds for young plaice are situated in areas where there are extensive tidal flats with abundant pools, as in the Wadden Seas of Germany and The
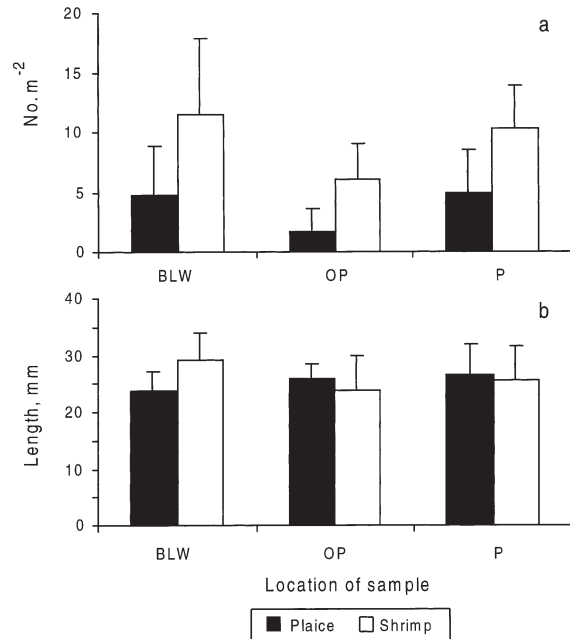

Fig. 10. *Pleuronectes platessa* and *Crangon crangon.* Mean (+1 SD) (a) abundances and (b) lengths inside and outside intertidal pools at Shenavallie. BLW: below low water mark; OP: outside pools; P: inside pools

Netherlands (Zijlstra 1972, Berghahn 1987) and on the east and west coasts of England (Riley et al. 1981). The suggestion that pools on sandy beaches, when present, can be used as refuges from predation can be compared with the situation in intertidal pools on some tidal marshes. There, young fishes remain in intertidal pools at low tide to avoid concentrations of predators in subtidal areas (Kneib 1987, 1997).

Predation risk for young plaice is size-dependent, so that any factor that increases growth rate will reduce the time that small fish are most vulnerable to predators. For most of the time that young plaice occupy shallow water, temperatures there are higher than in deeper water (Fig. 2), and higher temperatures are likely to result in higher growth rates. Possible differences in growth rate can be calculated using the equation $G = 1.3T + 1.7$, where G is growth rate in mm mo^{-1} and T is temperature in °C (Glazenburg 1983 in: Berghahn et al. 1995). In May, for example, when deeper water is at 8°C, then growth rates in shallow water would be approximately 10.7% higher for every °C that the temperature in shallow water exceeds that in deeper water. The temperature differences between the shallower and the deeper waters shown in Fig. 2 imply that the potential for faster growth in shallow waters is considerable. In the intertidal pools for several hours of the day during the warmer season, temperatures may be many degrees higher than sea tem-

peratures and fish in such pools may experience especially rapid growth. However, such a temperature-induced increase in growth could be counteracted by depletion of food reserves in the pools (Kneib 1994).

Occupation of different depths by small and large flatfishes gives access to different prey species, with potential consequences for growth rate. Polychaetes and amphipods were more abundant at greater depths at the study site (Burrows et al. 1994). These larger prey may be more profitable and allow a faster growth rate for larger fishes that are less vulnerable to predation.

Growth of individuals is accompanied by a gradual change in the distribution of the population. During and for a few weeks after the settlement period, the depth distribution remains more or less stable (Fig. 4). At this time fish transplanted from one depth to another quickly return to their original depth (R.N.G. pers. obs.). At the end of August, the median depth of the population increases, indicating that fish are moving into deeper water. This movement seems to involve the larger and presumably faster growing individuals, because few small individuals are found at the outer limits of the population's depth range. Not all large fish undergo this movement, however, because some can still be found in shallow water. The movement eventually results in a more uniform distribution of sizes in water <5 m so that the slope of the length-depth regression decreases and eventually becomes non-significant (Fig. 6). Such a redistribution can be interpreted, at least partially, as a response to the decrease in predation risk in deeper water conferred by the increase in size. It may also be hypothesised that the movement of larger individuals may be a reflection of a preference of larger individuals for the cooler temperatures offshore, because larger plaice grow more slowly than smaller plaice at higher temperatures (Fonds et al. 1992).

Behavioural preference for a particular depth is evident in juvenile plaice kept in laboratory tanks (Burrows 2001) and can explain much of the complex changes in distribution of these fish in shallow water over tidal and diel cycles (Burrows et al. 1994). Seasonal changes in median depths and changing size distributions with depth in plaice and dabs could therefore be explained if their depth preference changes with increasing length. As the fishes grow they may adopt the depth preference of their new size. Seasonal changes in median depths thus follow depth preferences of the median sizes (Fig. 7). As the smallest plaice grow in April and May, the median depth declines. When plaice reach sizes (>50 mm) that prefer greater depths, median depth of the population begins to increase (Fig. 4) and continues to do so through the rest of the year. Changes in the trend of size with depth can be understood by considering the effect of the

growth of a range of sizes of plaice in a population. In April and early May the plaice population consists of 15 to 30 mm individuals. The larger, and presumably older, fish are in shallower water than the smaller younger fish, so the trend of size with depth is negative (Figs. 5 & 6). When the median size reaches 30 to 35 mm, those smaller or larger than this size are found in deeper water, so there is no trend of size with depth. When the median size reaches 50 mm, larger fish are deeper and smaller fish are shallower, and so there is a positive trend of size with depth. The pattern of change in median depth and trend of size with depth seen in dab populations (Fig. 7) can probably be explained in the same way. In shrimp, however, no change in depth with size was apparent (Fig. 7). Shifts in the depth distribution of shrimp must occur therefore across all sizes. Both small and large individuals move from deeper (1.5 to 2.5 m) to shallower (1.0 m) water from March to June.

The discussion so far has centred on the importance of predation and temperature in controlling the distribution of juvenile plaice in an attempt to explain their restriction to very shallow water in the first few months after settlement. It has been argued that the advantages of such a restricted distribution lie in the ability to maximise growth and minimise predation risk. If this argument is valid for plaice, then the question arises of how 0-group dabs are able to survive using a very different settlement pattern. The 2 species are generally very similar in morphology, ecology and geographical distribution, and the main difference lies in their distribution in the first few months of life. Dabs settle widely in deeper water and are not restricted in their distribution at any stage of their life (Bolle et al. 1994). If, as argued above, plaice concentrate in shallow water to avoid the predators in deeper water, then what mechanism, if any, do dabs use to avoid the same predation pressure? Unfortunately the behaviour of dabs in this respect is unknown, and the answer to this particular question must remain speculative. The occupation of deeper water by young dabs, or conversely their avoidance of very shallow water, may be the result of a preference for lower temperatures than plaice. The detailed temperature preferences and tolerances of the 2 species are unknown. Nevertheless, some indication of their relative values may be gained from the observation that dabs do not migrate into the warmer waters of the intertidal zone (Edwards & Steele 1968, Poxton et al. 1983, Ansell & Gibson 1990). Furthermore, plaice have a more southerly distributional limit than dabs (Wheeler 1978). From this point of view, the utilisation of shallow water by plaice represents the occupation of a niche which not only reduces predation and maximises growth but also reduces competition for food in the earliest stages when densities are highest and com-

petition is likely to be greatest. Certainly, where the youngest individuals of the 2 species do overlap, their diets are very similar (Macer 1967, Edwards & Steele 1968, Ansell & Gibson 1990).

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