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SEASONAL, ANNUAL AND REGIONAL VARIATIONS IN ICHTHYOFAUNAL COMPOSITION IN THE INNER SEVERN ESTUARY AND INNER BRISTOL CHANNEL

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Monthly samples of fish from the intake screens of power stations at Oldbury and Berkeley in the inner Severn Estuary and Hinkley Point in the inner Bristol Channel, were used to analyse the community structures of the ichthyofauna in these regions. Marine species that use the estuary as a nursery area (marine estuarine-opportunists) were very abundant in the shallow inshore waters at Oldbury. Diadromous species were more abundant in the offshore and deeper waters at Berkeley than at Oldbury. Only one of the two species that complete their life cycles in the estuary was even moderately abundant in the inner estuary and the 15 freshwater species were relatively rare. Bass and particularly the sand goby complex were more numerous in the protected, inshore waters than the more offshore waters of the estuary. With the yellow and silver stages of the European eel, the reverse situation pertained. Seasonal changes in faunal composition were more pronounced in the inshore shallow than in more offshore deeper waters of the estuary. This largely reflected the sequential immigration of large numbers of the juveniles of marine estuarine-opportunist species into the former area for relatively short periods. Although the ichthyofaunal composition in the shallows at Oldbury underwent the same pattern of cyclical variation in each of five consecutive years, the degree of intra-annual variability differed, reflecting interannual differences in the recruitment strengths of the 0+ age classes of the different marine estuarine-opportunists. These cyclical changes were not correlated strongly with either salinity or water temperature. The faunal composition of the protected inshore, more marine waters of the inner Bristol Channel differed from those in both inshore and offshore regions of the inner estuary. The species which typified the fauna of the Channel were bib, poor cod, five-bearded rockling, sole and conger eel. Although the first four of these species were relatively more abundant in these waters than in the estuary, their juveniles often made extensive use of the shallows at Oldbury. This study emphasizes that, for some marine species, the protected inshore, and more marine, waters in the Bristol Channel can act as alternative nursery areas to those provided by the inshore shallows of the Severn Estuary.

INTRODUCTION

In terms of number of species, the estuarine ichthyofauna in temperate regions of both the northern and southern hemispheres is dominated by marine teleosts (Haedrich, 1983; Kennish, 1990; Potter et al., 1990). However, many of these teleosts, and also some elasmobranchs, enter estuaries irregularly and usually in low numbers, and are generally restricted to the seaward end of these systems. These species have been categorized as marine stragglers to contrast them from those marine species that typically enter estuaries for a period each year and often migrate upstream into areas where salinities are appreciably lower than full-strength sea-water (Lenanton & Potter, 1987). Estuaries, and particularly their shallow inshore waters, play such an important role as nursery areas for this latter group of fish that the species constituting this category have often been referred to as estuarine-dependent (e.g. Cronin & Mansueti, 1971; Blaber, 1987; Blaber et al., 1989). However, these species also often use protected and shallow inshore marine waters as nursery areas (Lenanton, 1982; Lenanton & Potter, 1987), and the transitory nature of estuaries, from a geological point of view, means that they could not be depended on as a critical area for the survival of marine species (Hedgpeth, 1982). For the latter two reasons, some workers have considered it more appropriate to refer to this category of fish as estuarine-opportunistic rather than estuarine-dependent (Lenanton & Potter, 1987).

Although estuaries also act as an essential route for diadromous fish during their migration from rivers to the sea and vice versa (McDowall, 1988), few of the true freshwater species are capable of surviving and spawning in these systems (Dando, 1984). The number of fish which are adapted to completing their life cycles in estuaries, and are subsequently referred to as estuarine species, is low, reflecting the problems that are posed to early life cycle stages by fluctuations in salinity, water movements and other variables, and again to the fact that, in their current form, these ecosystems are of relatively recent origin (McLusky, 1989; Whitfield, 1994). Recent years have seen a number of significant developments in the techniques for analysing and interpreting data on faunal communities, including those of estuaries (see Ter Braak, 1988; Belbin, 1993; Clarke & Warwick, 1994). During the same period, the contributions made by each of the different life cycle categories of fish described above, i.e. marine straggler, marine estuarine-opportunist, diadromous, estuarine and freshwater, have been quantified for the ichthyofauna of some estuaries in Australia, South Africa and North America (e.g. Loneragan et al., 1989; Potter et al., 1990, 1993; Yoklavich et al., 1991; Potter & Hyndes, 1994). No such data are available for estuaries in Europe.

The ichthyofauna of the Severn Estuary and the inner Bristol Channel, into which this estuary discharges, has been studied using samples collected from the cooling water intake screens of the Oldbury, Berkeley and Hinkley Point power stations between 1972 and 1977. These have provided data on the biology of the main species in the Severn Estuary and the way it is used by each species (see Claridge et al., 1986). Although some quantitative community analyses have been carried out on the data collected over five years from the relatively shallow and protected waters in the vicinity of the Oldbury Power Station in the inner Severn Estuary (Claridge et al., 1986; Potter et al., 1986), no comparable quantitative analyses have been undertaken on the data we collected for the fish fauna in the deeper waters at Berkeley in the inner Severn Estuary and in inshore marine waters at Hinkley Point in the inner Bristol Channel.

The present study uses contemporary techniques and approaches to analyse extensive data on the relative abundance of the different fish species in the Severn Estuary and inner Bristol Channel, in order to pose the following questions that are relevant to an understanding of the ichthyofauna of this region and of estuaries in general. Firstly, do marine estuarine-opportunists dominate the fish fauna of the shallows of the estuary to a greater extent than in either deeper estuarine waters or protected inshore and more marine waters in the channel? Secondly, are the faunal compositions in the estuary and channel most similar when the salinities are most similar? Thirdly, which species (and therefore also which life cycle categories) contribute most to any major differences in the faunal compositions at the three localities. Finally, what is the extent of intra- and interannual variations in faunal composition during the five years that sampling was undertaken at Oldbury, and are such variations related to physico-chemical variations and/or different recruitment patterns of the different fish species?

MATERIALS AND METHODS

The cooling water intake at the Oldbury Power Station is located near the shore of the inner Severn Estuary, whereas 7 km further upstream at the now decommissioned Berkeley Power Station, it was situated in the deep water channel of the estuary. The presence of a low man-made wall in the estuary at Oldbury retains water in the region at low tide. However, large volumes of estuarine water flow into and out of this region at other times in the tidal cycle, even allowing large numbers of benthic teleosts to enter and leave the area (Claridge et al., 1986). The Hinkley Point A Power Station is on the southern shore of Bridgwater Bay in the inner Bristol Channel, ~10 km downstream from the lower limits of the outer Severn Estuary. The cooling water at this station is drawn from inshore protected waters. The reader is referred to Claridge et al. (1986) for a map showing the locations of the above three Power Stations and the limits of the inner Severn Estuary and inner Bristol Channel, as designated by Radford & Joint (1980).

Fish were sampled from power station intake screens between July 1972 and June 1977 at Oldbury, from September 1974 to June 1977 at Berkeley and from September 1975 to May 1977 at Hinkley Point. Common and scientific names and life cycle categories for each species are given in Claridge et al. (1986). Fish were collected once weekly at the first two stations and once monthly at the third. Each weekly sample at Oldbury represented the catch taken over the previous 24 h. Samples at the other two stations had invariably been collected over more than several hours and sometimes for more than 24 h. The mean numbers of fish per daily sample were calculated for each month for Oldbury and Berkeley. Since the samples collected from each power station represent the material entrained on their screens over many hours, and as tidal water movement is very pronounced in the Severn Estuary and Bristol Channel, the fish in each sample were obtained from water that had been passing a considerable distance along the coast. Comprehensive details of the Oldbury and Berkeley Power Stations are given in Henderson (1989). The intake screens at Hinkley Point A Power Station were similar to those at Berkeley. From these data, it is evident that the maximum flow rates at the three stations are similar, i.e. 26·5 or 30 $m^3 s^{-1}$, and that the same is true for the screen mesh size, i.e. 9·5 or 10 mm. The effectiveness of using power station intake screens for obtaining representative samples of fish in an area is emphasized by the fact that 118 of the 122 fish species known to occur in the inshore waters of England and Wales were recorded from the screens of 12 power stations in those waters (Henderson, 1989). Salinities were measured at each of the three locations at the time of sampling and are expressed as monthly means for Oldbury or Berkeley, or given as the sole monthly

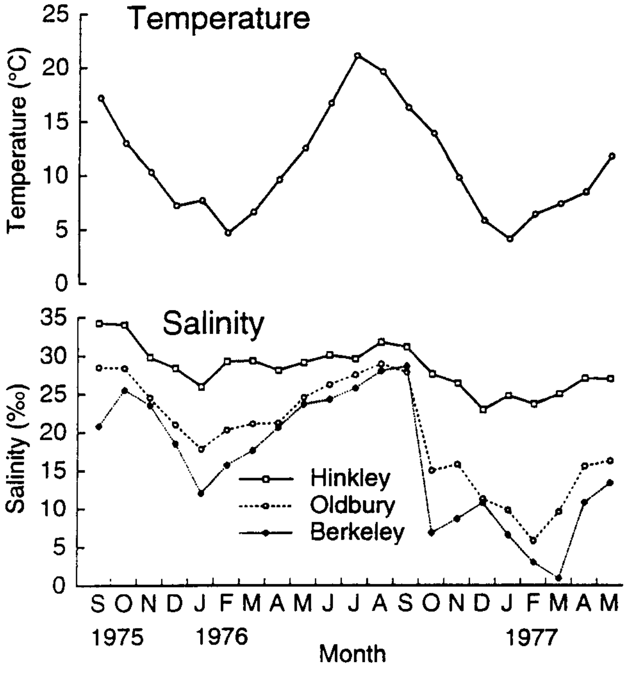

Figure 1. Mean monthly values for water temperatures at Oldbury, and salinities at Oldbury, Berkeley and Hinkley Point between September 1975 and May 1977.

value at Hinkley Point (Figure 1). Mean monthly water temperatures, derived from continuous records supplied by the Power Station Authorities, are given for Oldbury (Figure 1). The water temperatures at Oldbury tended to reach slightly higher levels in summer and decline to slightly lower levels in winter than was the case at Hinkley Point.

The percentage contributions made by the numbers of each species to the total catch of each sample at each power station were calculated for the period when all three stations were sampled, i.e. from September 1975 to May 1977. This adjustment of the data to percentage contributions is necessary because the catch periods at Berkeley and Hinkley varied, and thus the total abundance figures for these two stations are not directly comparable with those at Oldbury. In fact, deliberate exclusion of information on changes in total abundance is sometimes desirable, since it can be a source of uncontrolled variability of little interpretational significance in a multivariate analysis, the strength of which is in detecting subtle but important shifts in the balance of species within a community (Clarke & Warwick, 1994).

The respective percentage contributions of each species at the three stations in each month between September 1975 and May 1977 were classified by hierarchical agglomerative clustering, using group average linking, and ordinated using multidimensional scaling techniques on the PRIMER package (Clarke & Warwick, 1994). Prior to classification and ordination, the Bray-Curtis similarity measure was used to produce the association matrix. Analysis of similarities (ANOSIM) was used to test for differences between the groups of samples from Oldbury, Berkeley and Hinkley Point, and similarity percentages (SIMPER) were employed to determine the species most responsible for the Bray-Curtis dissimilarity between groups (Clarke, 1993). Salinity and temperature were correlated with the biotic dissimilarity values, employing BIOENV and using weighted Spearman's rank correlations (Clarke & Ainsworth, 1993). Multivariate dispersion (MVDISP) was used to determine the degree of dispersion of the samples from the three different stations (Somerfield & Clarke, 1997). The number of individuals of each species caught at Oldbury in each month between July 1972 and June 1977 were expressed as mean monthly catches per 24 h and then fourth root transformed, the latter ensuring that the multivariate analysis is not excessively dominated by the most abundant species (Clarke & Green, 1988). The species compositions for this five year data set and for each 12 month period, i.e. July–June, were ordinated as described above.

RESULTS

Water temperatures and salinities

Mean monthly water temperatures at Oldbury declined continuously from 17·2°C in September 1975 to 4·7°C in February 1976, before rising progressively to a maximum of 21·1°C in July 1976 (Figure 1). Temperatures subsequently declined to a minimum of 4·1°C in January 1977.

Salinities at Hinkley Point fell from 34‰, i.e. close to full-strength sea-water, in September and October 1975, following a very dry summer, to a minimum of 26‰ in January 1976 (Figure 1). They subsequently lay just below 30‰ through to July 1976, and then rose to just over 32‰ in August. Salinities then declined to a minimum of 23‰ in December 1976, before increasing to ~27‰ in April and May 1977 (Figure 1).

Salinities underwent far more pronounced changes at Oldbury and Berkeley in the inner Severn Estuary than at Hinkley Point in the inner Bristol Channel (Figure 1). However, while salinities followed similar seasonal trends at Oldbury and Berkeley, they declined to far lower levels in the second year than in the first year at both sites and, in all but one month, were higher at Oldbury than at Berkeley, a further 7 km upstream. These features are illustrated by comparing the minimum salinities at the two stations. Thus, in the first year, salinities declined to minima of 17·8‰ at Oldbury and 12·0‰ at Berkeley, both of these values being recorded in January 1976, whereas in the second year they fell to a minimum of 5·8‰ at Oldbury and 0·9‰ at Berkeley, these values being recorded in February and March 1977, respectively. In 1976, salinities rose to a maximum of ~29‰ at both estuarine stations in late summer/early autumn, a value similar to that recorded at Oldbury in the early autumn of the previous year.

Relative abundance of major species

A total of 73, 65 and 64 species were recorded at Oldbury, Berkeley and Hinkley Point, respectively, during the 21 months between September 1975 and May 1977 when all three stations were sampled (Table 1). The three most abundant species contributed far more to the numbers at Oldbury (70·5%) and Berkeley (68·0%) than at Hinkley Point (42·5%). Whiting was the most abundant species at Oldbury and Hinkley Point and the

Table 1. *Life cycle category and the number of individuals of the 15 most abundant species, together with their percentage contributions, at Oldbury, Berkeley and Hinkley Point between September 1975 and May 1977. The corresponding rank of each species at Oldbury is also given for the latter two stations. The numbers for each species represent the sum of the mean numbers of fish per sample in each month at Oldbury and Berkeley and the sum of the fish in the single samples collected in each month at Hinkley Point.*

	Oldbury				Berkeley					Hinkley Point			
	Category	N	%		Category	N	%	Oldbury		Category	N	%	Oldbury
Whiting	O	6393	34·7	Flounder	O	1360	23·0	4	Whiting	O	714	23·6	1
Sand goby complex	O	4148	22·5	Whiting	O	1340	22·7	1	Poor cod	O	362	12·0	6
Bass	O	2468	13·4	European eel	D	1325	22·4	9	Flounder	O	210	6·9	4
Flounder	O	1062	5·8	Thin-lipped grey mullet	O	284	4·8	5	Thin-lipped grey mullet	O	194	6·4	5
Thin-lipped grey mullet	O	863	4·7	Sand goby complex	O	243	4·1	2	Five-bearded rockling	O	188	6·2	26
Poor cod	O	714	3·9	Sea snail	O	188	3·2	8	Sea snail	O	170	5·6	8
Twaite shad	D	701	3·8	Twaite shad	D	145	2·5	7	Bib	O	165	5·5	15
Sea snail	O	554	3·0	Bass	O	137	2·3	3	Sole	O	157	5·2	17
European eel	D	373	2·0	Atlantic salmon	D	129	2·2	24	Bass	O	127	4·2	3
Herring	O	222	1·2	Poor cod	O	113	1·9	6	Twaite shad	D	96	3·2	7
River lamprey	D	132	0·7	Herring	O	85	1·4	10	Conger eel	S	91	3·0	31
Common goby	E	117	0·6	Northern rockling	O	64	1·1	16	Lumpsucker	S	74	2·4	58
Sprat	O	109	0·6	Sprat	O	61	1·0	13	Pollack	O	61	2·0	22
Three-spined stickleback	F	94	0·5	Sole	O	58	1·0	17	European eel	O	46	1·5	9
Bib	O	89	0·5	Norway Pout	S	48	0·8	20	Sprat	O	43	1·4	13
Total number of fish		18447	98·3			5916	94·3				3025	89·2	
Total number of species		73				65					64		

D, diadromous; E, estuarine; F, freshwater; O, estuarine opportunist; S, marine straggler.

second most abundant at Berkeley, contributing between 22·7 and 34·7% to the total catch at these three stations (Table 1). The sand goby complex made a far greater contribution at Oldbury (22·5%), where it was the second most abundant species, than at either Berkeley (4·1%) or Hinkley Point (1·3%), where it ranked fifth and sixteenth, respectively. Likewise, bass made a far greater contribution at Oldbury (13·4%) than at either Berkeley (2·3%) or Hinkley Point (4·2%). Flounder contributed far more to the total numbers at Berkeley (23·0%), where it was the most abundant species, than at either Oldbury (5·8%) or Hinkley Point (6·9%). The European eel comprised 22·4% of the catch at Berkeley, which was over ten times its relative contribution at either of the other two stations (Table 1). Poor cod was the second most abundant species at Hinkley Point, contributing 12·0% to the catch, compared with 3·9% at Oldbury and 1·9% at Berkeley. Thin-lipped grey mullet, twaite shad and sea snail each ranked in the top ten most abundant species in samples from each of the three stations (Table 1).

The river lamprey and common goby were caught in appreciable numbers at Oldbury, but were rarely or never recorded at Berkeley and Hinkley Point (Table 1). The Atlantic salmon, represented by smolts, contributed over 2% to the samples at Berkeley, but was relatively rare at Oldbury and was never recorded at Hinkley Point. Five-bearded rockling, bib, sole, conger eel, lumpsucker and pollack were all relatively more abundant at Hinkley Point than at either Berkeley or Oldbury.

Life cycle categories

Nine of the marine species of fish collected from the protected inshore waters at Hinkley Point in the inner Bristol Channel were not obtained from either the inshore estuarine waters at Oldbury or the more offshore and deeper waters at Berkeley in the inner Severn Estuary in the 21 months between September 1975 and May 1977, when all three stations were sampled. However, none of these species, which included four elasmobranchs, was even moderately abundant at Hinkley Point, collectively contributing <1% to the total number of fish.

In terms of number of species, the marine stragglers, i.e. those species found irregularly and in small numbers in estuaries, contributed 44·6% at Berkeley and 52·1% at Oldbury (Table 2). However, the contribution of this category to the total catch of fish was far greater at Hinkley Point (11·9%) than at either Berkeley (2·8%) or Oldbury (0·7%). Although there were only 15 marine estuarine-opportunist species, they contributed 91·3% to the total fish catch at Oldbury and were also the most important category at Berkeley and Hinkley Point. The common goby and sand smelt, which can complete their life cycles in estuaries, together contributed only 0·7% to the total catch of fish at Oldbury, and even less at Berkeley (0·3%) and Hinkley Point (0·2%). The diadromous category, which comprised mainly the anadromous river lamprey and twaite shad and the catadromous European eel, contributed 28·0% to the numbers of fish caught at Berkeley, compared with 6·6% at Oldbury and 5·0% at Hinkley Point. Only two freshwater species were recorded at Hinkley Point, compared with 12 at Oldbury and 13 at Berkeley. The contribution of freshwater species to the total catch was only 1·8% at Berkeley and 0·6% at Oldbury and was negligible at Hinkley Point (Table 2).

Table 2. *Number of species and individuals of each life cycle category, together with their percentage contributions, recorded for samples collected from each of the three Power Stations between September 1975 and May 1977. The numbers for each category represent the sum of the mean numbers of fish per sample in each month at Oldbury and Berkeley and the sum of the fish in the single samples collected in each month at Hinkley Point.*

Number of species

	Oldbury		Berkeley		Hinkley Point	
Category	N	%	N	%	N	%
Marine	–	–	–	–	9	14·1
Marine straggler	38	52·1	29	44·6	31	48·4
Estuarine opportunist	15	20·5	14	21·5	15	23·4
Estuarine	2	2·7	2	3·1	2	3·1
Diadromous	6	8·2	7	10·8	5	7·8
Freshwater	12	16·4	13	20·0	2	3·1
All	73		65		64	

Number of individuals

	Oldbury		Berkeley		Hinkley Point	
Category	N	%	N	%	N	%
Marine	–	–	–	–	27	0·9
Marine straggler	134	0·7	168	2·8	361	11·9
Estuarine opportunist	16841	91·3	3973	67·2	2479	82·0
Estuarine	132	0·7	16	0·3	5	0·2
Diadromous	1222	6·6	1655	28·0	150	5·0
Freshwater	118	0·6	104	1·8	3	0·1
All	18447		5916		3025	

Classification and ordination of samples from the three stations

Classification separated the samples into two major divisions, designated A and B in Figure 2. All of the 21 samples from Berkeley, except those collected in October, November and December of 1976, are in division A. Furthermore, all but one of the 18 Berkeley samples in division A form a discrete group (C in Figure 2). The other two main groups in division A (D&E in Figure 2) each consist almost entirely of samples collected from Oldbury. Group D contains late spring and early summer samples, while Group E comprises samples from Oldbury in late winter/early spring. Only one sample from Hinkley Point, i.e. August 1976, is located in division A.

Within division B, the samples collected from both Berkeley and Oldbury in October, November and December 1975 form a discrete group, together with samples from Oldbury in September 1975 and October and November 1976 (F in Figure 2). The other two major groups (G&H in Figure 2) consist solely of samples from Hinkley Point. Group G consists almost exclusively of autumn and winter samples, while Group H contains spring and summer samples. A final group (I) within Division B contains four Oldbury samples, three of which are from winter.

In the ordination plot shown in Figure 3, the points for the samples from Oldbury between September 1976 and March 1977 all lie below those from Berkeley and Hinkley Point, and points from the same station from April to July 1976 all lie above those from

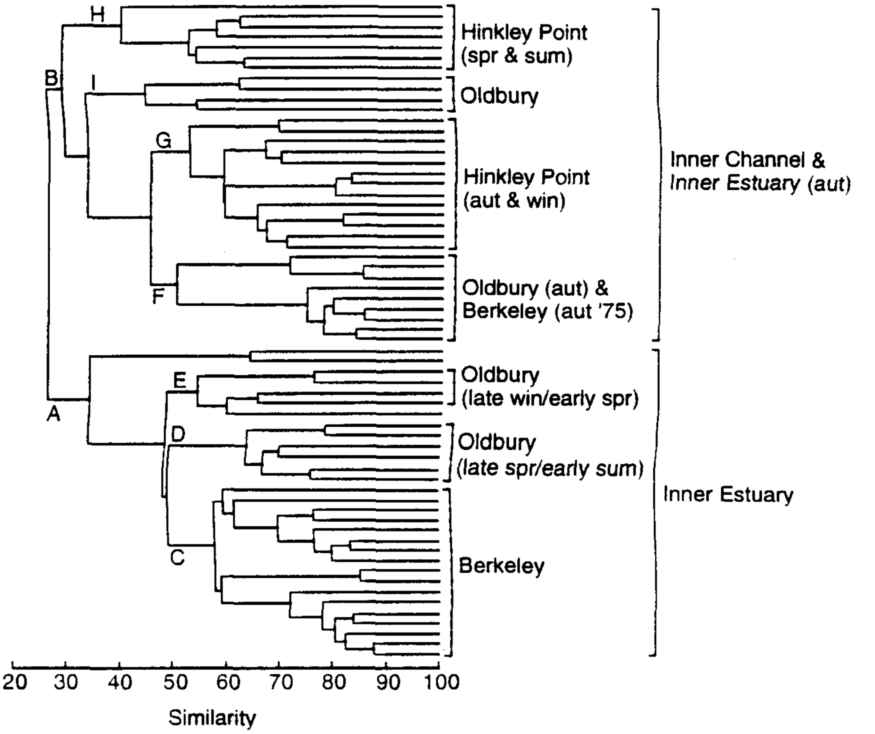

Figure 2. Classification of species percentage contribution data for samples collected from Oldbury, Berkeley and Hinkley Point between September 1975 and May 1977.

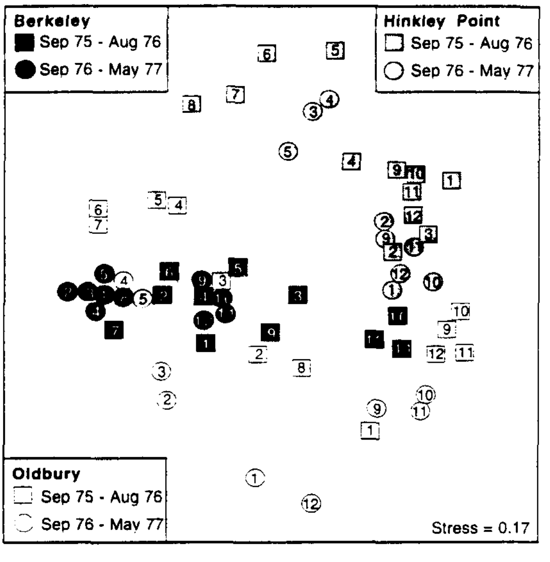

Figure 3. Ordination of species percentage contribution data for samples collected from Oldbury, Berkeley and Hinkley Point between September 1975 and May 1977. Numbers correspond to months of the year.

Berkeley. Points for Oldbury in March 1976 and April and May 1977 lie amongst the relatively tight cluster comprising the vast majority of the samples from Berkeley. The samples collected from Oldbury and Hinkley Point between early autumn and the middle of winter of both years formed a broad vertical cluster on the right of the ordination plot, together with those from Berkeley in October–December 1975 (Figure 3). Samples from Oldbury in September–December 1975 lie close to those from Berkeley in October–December of the same year and to those from Hinkley Point in October–December 1976 and January 1977. However, none of the points for Hinkley Point overlap those of either Oldbury or Berkeley (Figure 3).

Analysis of similarities showed that there was a significant overall difference between the compositions of the ichthyofauna at Oldbury, Berkeley and Hinkley Point, and that the compositions differed significantly in comparisons between all three pairs of sites. Similarity percentages (SIMPER) showed that the main overall discriminating species, that were consistent for each pairwise comparison between stations, were sand goby complex and bass for Oldbury, European eel for Berkeley, and bib, poor cod, sole, five-bearded rockling and conger eel for Hinkley Point.

Superimposition of salinities on the points for the mean monthly species percentage composition data for samples showed that there was no overall consistent relationship between faunal composition and salinity (Figures 3 & 4). However, all but two of the ten samples from the autumn and early winter of 1975 at Oldbury and Berkeley clustered together with those from the corresponding period of the following year at Hinkley Point, when salinities likewise generally lay between 21 and 28‰ (Figures 3 & 4). In contrast, the temperatures for the months when these samples were taken showed far greater variability, ranging from a low of 4°C to a high of 17°C (Figures 3 & 4).

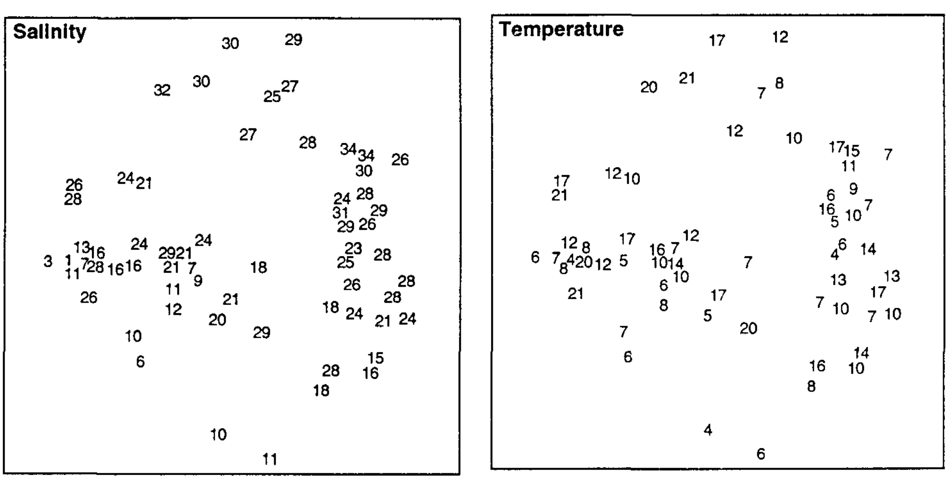

Figure 4. Superimposition of mean salinities and temperatures on the corresponding ordination points for the samples collected from Oldbury, Berkeley and Hinkley Point between September 1975 and May 1977 and shown in Figure 3.

The degree of scatter of the monthly samples is far greater at Oldbury than at either Berkeley or Hinkley Point (Figure 3). However, in defining the variability within a group of samples, it can be misleading to use the inter-sample distances on the MDS ordination itself. Unless the stress is near zero, which is not the case on this occasion, this two-dimensional view of the higher dimensional data will undergo some distortion. The apparent differences in variation between Oldbury, Berkeley and Hinkley Point are quantified more precisely using MVDISP, as described in Somerfield & Clarke (1997). In this routine, a series of values reflecting relative variation within the groups is calculated from the similarity values underlying the MDS. This 'relative dispersion sequence' uses the average rank similarity within each group (having ranked the Bray-Curtis matrix, ignoring all between-group similarities). The values are standardized so that similar seasonal variability within each group yields dispersion values of around unity. Here, this is very far from the case, with an increasing dispersion sequence from Berkeley (0·74), to Hinkley Point (0·99) and then Oldbury (1·27) (Table 3), confirming that the visual impression from the ordination for the same 21 month period is correct (Figure 3). Separate ordination of the data sets for Oldbury, Berkeley and Hinkley Point, which overcomes the problems of using the inter-sample distances of the composite data set, shows that the composition of the fauna at these three sites undergoes sequential changes, which at Oldbury and Hinkley Point are cyclical and annual (Figure 5). Analysis of all the data available for the three sites, i.e. 60 months from Oldbury, 35 months from Berkeley and 21 months from Hinkley Point, reveals that intra-annual variability was greatest in the three later years at Oldbury, and was least in one of the years at Berkeley, i.e. July 1976 to June 1977 (Table 3).

Table 3. *Dispersion values for ordination plots for Oldbury and Berkeley in the inner Severn Estuary and Hinkley Point in the inner Bristol Channel in different years.*

Period	Power station		
	Oldbury	Berkeley	Hinkley
September 1975–May 1977	1·27	0·74	0·99
July 1972–June 1973	1·00	–	–
July 1973–June 1974	0·98	–	–
July 1974–June 1975*	1·15	1·11	–
July 1975–June 1976†	1·24	0·98	0·90
July 1976–June 1977‡	1·26	0·35	1·04

*, sampling at Berkeley started in September; †, sampling at Hinkley Point started in September; ‡, sampling at Hinkley Point ended in May.

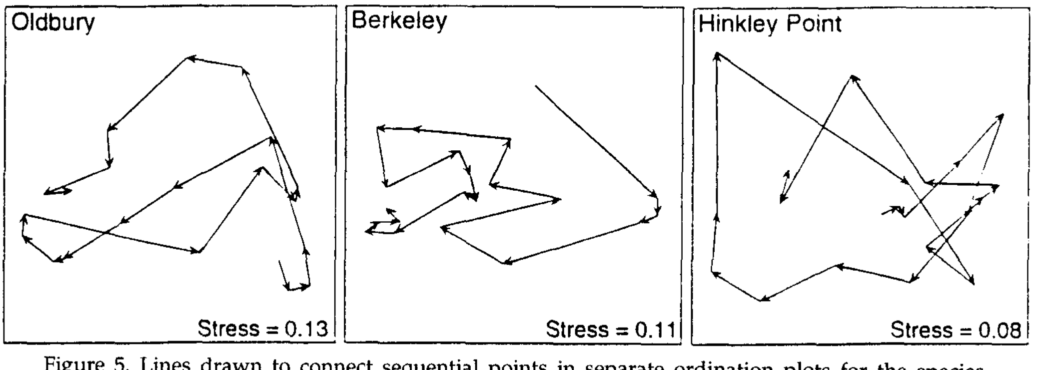

Figure 5. Lines drawn to connect sequential points in separate ordination plots for the species percentage contribution data for samples collected from Oldbury, Berkeley and Hinkley Point between September 1975 and May 1977.

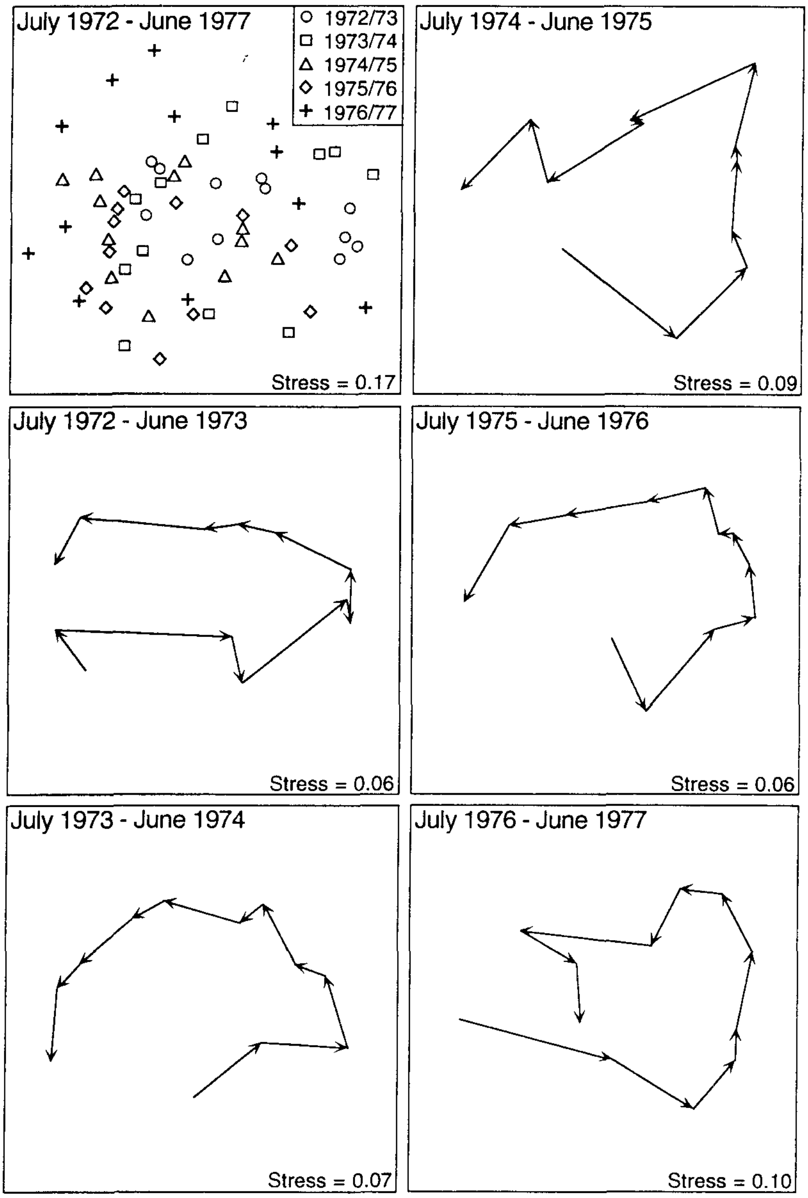

Figure 6. Ordination of the abundance data for Oldbury between July 1972 and June 1977 and for each of the sequential 12 months within this period. Ordinations of each of the five 12 month intervals were carried out independently on their respective abundance data. Lines are drawn between points for sequential monthly samples.

Interannual changes in faunal composition at Oldbury

On ordination plots, the points corresponding to the mean monthly abundance data for species in samples from Oldbury between July 1972 and June 1977, showed a similar cyclical trend in each of the five successive 12 month periods (Figure 6). Analysis of similarities demonstrated that the composition of the faunas in the five years were significantly different and that, except for 1974/1975 versus 1975/1976, each of the ten pair-wise comparisons between years were significantly different. BIOENV showed that the biotic dissimilarity values were not strongly correlated with salinity in any of the five consecutive 12 month periods at Oldbury, with ρ ranging from only 0·09 to 0·34. Although the ρ values for temperature in each year were higher than those for salinity in four of the five years (0·24–0·48), they still indicate that there was also not a strong correlation with this environmental variable. When salinity and temperature were combined in the analysis, the ρ values did not improve, with values for the five years ranging from 0·20 to 0·44. There was also not a strong correlation with either salinity or temperature when the data sets for each of the five years were pooled (ρ=0·29 and 0·12, respectively), and when these two variables were combined in the analysis for these pooled data (ρ=0·27).

DISCUSSION

Faunal composition of the inner estuary

The present study has demonstrated that, in the 21 months between September 1975 and May 1977, the composition of the ichthyofauna in the inshore shallows at Oldbury and the more offshore and deeper waters at Berkeley in the inner Severn Estuary were both distinct from that in protected inshore waters at Hinkley Point in the inner Bristol Channel. Although samples from four months at Oldbury lay within a cluster on the ordination plot, which contained the majority of the Berkeley samples, the faunal compositions at these two inner estuary localities were also significantly different from each other.

The fauna at Oldbury was dominated by the presence of very large numbers of the juveniles of several marine estuarine-opportunist species, thereby emphasizing the role that shallow, inshore estuarine environments play in the life cycle of these marine fish species. Indeed, these species were so abundant at Oldbury that they contributed over 91% to the total catch of fish at that station. Previous studies have demonstrated that the most abundant of these marine estuarine-opportunist species were whiting, bass, flounder, thin-lipped grey mullet, poor cod, sea snail, herring, sprat and the complex of two sand goby species (Badsha & Sainsbury, 1978; Titmus et al., 1978; Claridge & Potter, 1983, 1984, 1985; Potter & Claridge, 1985; Claridge et al., 1985, 1986; Hardisty & Badsha, 1986; Potter et al., 1988). The fact that the two marine species comprising the sand goby complex were far more abundant in the protected shallow waters at Oldbury than in the deeper estuarine waters at Berkeley, is consistent with the conclusion that gobies, when found in estuaries, prefer shallow and calmer waters (Gill & Potter, 1993).

Since estuaries are highly productive ecosystems (Schelske & Odum, 1970) and thereby facilitate the rapid growth of juvenile fish, it is relevant that the inshore shallows of the Oldbury region contain high densities of small crustaceans, which are an important food source for juvenile fish in the region (Moore & Moore, 1976; Moore et al., 1979; Henderson et al., 1992). The important role played by the shallows of the Severn Estuary as a nursery ground for certain marine species parallels the situation recorded in temperate estuaries elsewhere in the Northern Hemisphere and also in the Southern Hemisphere (e.g. Deegan & Thompson, 1985; Loneragan et al., 1986; Yoklavich et al., 1991).

Since adults of the river lamprey were relatively far more abundant at Oldbury than Berkeley, they presumably migrate upstream along the sides of the estuary, where the flow is slowest. Such a pattern of migration would be consistent with the fact that adult lampreys are poor swimmers (Beamish, 1974).

Faunal composition in offshore, deeper waters in the inner Severn Estuary

The far lower total catch of marine estuarine-opportunists at Berkeley than Oldbury (3973 vs 16841), and their far lower contribution to the numbers of fish at the former station (67·2% vs 91·3%), are consistent with the results of studies in other estuaries, which have likewise indicated that the juveniles of larger marine fish species tend to occupy shallow waters and then move offshore and out to sea as they increase in size (Chubb et al., 1981; Ruiz et al., 1993; Hyndes et al., 1996). It is also noteworthy that juveniles and adults of the anadromous twaite shad, downstream migrating Atlantic salmon smolts, and, more particularly, the yellow and silver representatives of the catadromous European eel, were all caught in reasonable numbers in the midstream waters at Berkeley. The abundance of the above three species at Berkeley accounts for the fact that the diadromous category contributed over a quarter of the fish caught at this deeper water location.

Although classification separated the Berkeley samples from those at Oldbury in most months, this was not the case on several occasions during the autumn and early winter of 1975. The samples from both stations in this period also lay close together on the ordination plot. Examination of the raw catch data for that period showed that the ichthyofauna in the shallow and deeper waters of the estuary both contained large numbers of whiting and, to a lesser extent, thin-lipped grey mullet, bass and poor cod.

No freshwater species were abundant at either Berkeley or Oldbury, paralleling the situation typically found in estuaries (Dando, 1984), and the common goby was the only estuarine species that was even moderately numerous at these stations (Claridge et al., 1985, 1986).

Faunal composition of inshore waters of the inner Bristol Channel

The importance of shallow waters as a nursery area for marine species is emphasized by the observation that the marine estuarine-opportunist category, again represented largely by juvenile fish, made a large contribution (82%) to fish numbers at Hinkley Point. Indeed, each of the species of marine estuarine-opportunist found at Oldbury was also recorded at Hinkley Point. The presence at Hinkley Point of considerable numbers of the juveniles of all of those marine species, that were likewise abundant as juveniles in the Severn Estuary, demonstrates that, for several species, protected inshore, and more marine, waters act as alternative nursery areas to inshore, sheltered estuarine waters, both in south-west England (see also Henderson & Holmes, 1991; Henderson & Seaby, 1994) and elsewhere (e.g. Potter et al., 1990). This supports the view that, for such species, the term estuarine-opportunist is more appropriate than estuarine-dependent (see Lenanton & Potter, 1987).

The species which discriminated the samples from Hinkley Point from those at Oldbury and Berkeley included bib, five-bearded rockling, sole and poor cod which, although belonging to the estuarine-opportunist category, made a relatively greater contribution to the samples from the Bristol Channel than to those from the estuary. However, poor cod is found in large numbers in the shallows of the inner Severn Estuary (Claridge & Potter, 1984), and thus does not belong to a group that tends to avoid estuaries, as alleged by Henderson (1989). The conger eel, which was the fifth discriminating species for Hinkley Point, was only occasionally caught in the inner estuary and then mainly in the dry summer of 1976. It is also relevant that nine of the marine species recorded at Hinkley Point were found at neither Oldbury nor Berkeley. Furthermore, species evenness was greater at Hinkley Point than at the other two stations, with the three most abundant species contributing <43% to the catch at this station, but >68% at Oldbury and Berkeley.

Factors influencing community structure

As shown earlier, the composition of the ichthyofauna varied between inshore, shallow and more offshore deeper waters in the estuary and between these two areas and the inshore, protected waters at Hinkley Point outside the estuary. The strong and consistent cyclical changes in faunal composition in the shallow waters at Oldbury are related in particular to the sequential immigration of large numbers of the juveniles of the different marine species for short periods. Thus, these faunal changes are driven mainly by the time at which the various marine species spawn and the time that is taken by their larval or juvenile stages to be recruited into the shallows of the estuary. As a result of their particular recruitment patterns, flounder peaked in abundance in the estuary in July, sprat and herring in August, bass in September, poor cod, bib and whiting in October, thin-lipped grey mullet in November, and sea snail in December (Claridge et al., 1986). These sequential changes are enhanced by increased numbers of the three-spined stickleback, a freshwater species, during autumn and winter as freshwater discharge increased towards its peak in winter (Potter et al., 1986). The above species correspond to a group identified by Henderson (1989), on the basis of principal component analyses, as comprising species which are abundant in low salinity conditions in the upper reaches of estuaries. In terms of cyclical changes, it is also relevant that, in each year, large numbers of the anadromous river lamprey migrated up through the estuary between the autumn and early spring (Abou-Seedo & Potter, 1979).

Although the composition of the ichthyofauna at Oldbury underwent similar cyclical changes in each year, the amount of intra-annual variation differed between years and the composition of the fauna in any one year almost invariably differed from those in each of the other years. Examination of the abundance data for the main species between July 1972 and June 1977, indicate that these differences largely reflect the fact that, firstly the recruitment strengths of the juveniles of each of the marine estuarine-opportunist species varied markedly among years, and secondly the years when recruitment was strongest often differed among species. Some idea of the magnitude of the differences in relative recruitment strengths between years and species is provided by the fact that the maximum annual abundances (July–June) were attained by bass in 1976–1977, by bib in 1974–1975 and by poor cod in 1975–1976 and that, for each of these species, the abundance in these years was at least one order of magnitude, and in one case two orders of magnitude greater than in the years of least abundance (Claridge & Potter, 1983, 1984; Claridge et al., 1986).

Since the main marine species, and also the diadromous species and three-spined stickleback, were each abundant in the shallows of the upper estuary for only a restricted period of time, the maximum abundance of each of these species will obviously be measurably associated (but not necessarily causally associated) with the temperature and salinity of that region at the time when it typically occurs there. As each of these species also usually enters the estuary at a similar time each year, the faunal composition in the late summer and early autumn, when temperatures and salinities reach their maxima (Claridge & Potter, 1984), will likewise be associated with the temperatures and salinities found during that period. However, the sequential immigration and emigration of the main species throughout the year means that, when similar temperatures and salinities occur at quite different times of the year, e.g. mid to late spring and mid to late autumn, the faunal composition during these two periods will differ markedly. It is thus not surprising that the ichthyofaunal composition of the inner Severn Estuary was not strongly correlated with either temperature or salinity.

Although changes in the composition of the ichthyofauna in the upper estuary largely reflect the different times of recruitment of the abundant species, there is still evidence that, at certain times, community structure can also be modified to some degree by salinity. For example, the faunas in the inner estuary and inner channel were most similar during a period when salinities were also similar. Thus, the ichthyofaunal samples at Oldbury and Berkeley in the dry autumn and early winter of 1975 were similar to those in the corresponding period at Hinkley Point in the following wetter year, when salinities were likewise between 21‰ and 28‰. This similarity reflects a particularly marked tendency for the juveniles of certain marine estuarine-opportunist species, e.g. whiting, poor cod, bib and thin-lipped grey mullet, to migrate into both regions during the above two autumn/early winter periods, and for marine species in general to remain longer in the estuary during the former and drier of these two periods.

In the context of the influence of environmental variables, it is noteworthy that, during the greatest period of freshwater discharge encountered during this study, when salinities declined to <6‰ at Oldbury and <1‰ at Berkeley, the marine species eventually disappeared from the upper estuarine waters in the region of these two stations. Furthermore, the decline in whiting abundance was far more pronounced in the very wet autumn of 1976/1977, when salinities declined to particularly low levels, than in other years (Potter et al., 1988). At the same time, small numbers of freshwater fish, such as roach, bronze and silver bream, perch, rudd, crucian carp and particularly the three-spined stickleback, appeared in this region, presumably having been flushed down from the riverine areas. Considerable numbers of the common goby, an estuarine species, were also caught during these periods of very high freshwater discharge.

In summary, the results of the present paper, allied with previous analyses of seasonal and annual changes in abundance of the most numerous fish species in the Severn Estuary, have provided information on the composition of the ichthyofauna of this estuary and for the basis for intra- and interannual differences in that composition. There is thus now strong evidence that such differences are related largely to the relative strengths of recruitment of the juveniles of marine species, which in turn will have ultimately been determined by such features as reproductive success, distance from spawning ground, larval survival and the efficiency of larval and juvenile transport mechanisms. Salinity can have a moderating influence on the ichthyofaunal composition of estuaries. For example, some freshwater species are flushed downstream into the inner estuary during heavy freshwater discharge in winter, and some stenohaline marine species are found in the inner estuary in summer, when salinities are high. However, no species of either of the latter two groups was abundant in the estuary. Our results also emphasise that, while the shallows of estuaries are very important nursery areas for some marine species of fish, the same species also often use protected, and more inshore, marine waters in the channel for this purpose.

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