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Fish fauna of the Severn Estuary. Are there long-term changes in abundance and species composition and are the recruitment patterns of the main marine species correlated?

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Abstract

Fish were collected from the intake screens of the Oldbury Power Station in the Severn Estuary in each week between early July 1972 and late June 1977 and at least twice monthly between early January 1996 and late June 1999. The annual catches, after adjustment to a common sampling effort, demonstrate that the abundance of fish at Oldbury was far greater in the 1990s than 1970s, mainly due to marked increases in the numbers of certain marine species, such as sand goby, whiting, bass, thin-lipped grey mullet, herring, sprat and Norway pout. These increases may reflect the great improvement that occurred in the water quality of the Severn Estuary between these decades. The only species that declined markedly in abundance was poor cod. Modest declines in flounder and River lamprey paralleled those occurring elsewhere in the UK. The species composition in the two decades also differed, reflecting changes not only in the relative abundances of the various marine estuarine-opportunistic species, which dominated the ichthyofauna, but also in those of the suite of less abundant species in the estuary. The cyclical changes undergone each year by the species composition of the fish fauna of the Severn Estuary reflect sequential intra-annual changes in the relative abundances of species representing each of the marine, diadromous and freshwater categories. New approaches have been developed to test whether or not large sets of correlations between patterns of recruitment amongst abundant marine

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species (internal correlations), and between those patterns and salinity and water temperature within the estuary (cross-correlations), were significant. The correlation profile analyses found no evidence that the annual recruitment strengths of these species were either intercorrelated, or correlated with either one or a combination of both of the above environmental variables. Yet, the timings of the recruitment of these species into the estuary were intercorrelated, i.e. a slightly earlier or later than normal immigration by one species in a given year was paralleled by the same trend in other species. However, this association in recruitment times could be linked neither to salinity nor water temperature within the estuary, nor to a combination of these two variables. These results indicate that, while the factors that influence the annual recruitment strengths of the juveniles of different marine species vary, inter-annual differences in the phasing of events that regulate spawning times and/or larval dispersal influence, in the same direction, the times when marine species are recruited into the estuary.

Keywords: Annual cyclical changes; Correlation profile analyses; Environmental variables; Estuary; Fish; Long-term changes; Recruitment; Species compositions and abundances

1. Introduction

The fish faunas of estuaries in temperate regions of the northern hemisphere are dominated by marine species (Haedrich, 1983; Dando, 1984; Elliott and Dewailly, 1995), which can be categorised as either marine stragglers or marine estuarine-opportunists (Potter et al., 1997). The marine stragglers are defined as those species that typically occur irregularly and in low numbers in estuaries and usually near their mouths where salinities are relatively high. In contrast, the marine estuarine-opportunists comprise those euryhaline species which enter estuaries in large numbers and sometimes penetrate far upstream into regions of reduced salinity (e.g. Henderson, 1989). Although macrotidal estuaries in the northern hemisphere act as important nursery areas for certain marine estuarine-opportunists (e.g. Gunter, 1961; Haedrich, 1983; Maes et al., 1998), relatively few species are able to spawn and complete their life cycles in these systems (Dando, 1984; Kennish, 1990).

Large numbers of the juveniles of certain marine estuarine-opportunist species are recruited into nearshore waters of the Severn Estuary (UK) (Claridge et al., 1986; Potter et al., 1997). The more abundant of these species typically breed at some time between late winter and early summer and, from the distribution of their larvae (Russell, 1980), most of these spawn either within or just outside the Bristol Channel into which the Severn Estuary discharges. Weekly sampling in the Severn Estuary between July 1972 and June 1977 has provided data on the abundance, time of occurrence and size composition of each of the more numerous fish species present during that period (Claridge and Gardner, 1977, 1978; Claridge and Potter, 1983, 1984, 1985, 1987, 1994; Claridge et al., 1985; Badsha and Sainsbury, 1978; Titmus et al., 1978; Abou-Seedo and Potter, 1979; Hardisty and Badsha, 1986; Potter and Claridge, 1985; Potter et al., 1988).

Since the Severn Estuary used to be exposed to the input of large amounts of certain contaminants, and particularly of highly toxic elements such as cadmium (Little and Smith, 1994), such contamination may have led to the mortality of some fish. If that was the case, the marked decline in the input of those contaminants into the Severn Estuary during the last 20–30 years (Little and Smith, 1994; Vale and Harrison, 1994; Anon, 1997, 1999) might then have led to an increase in the abundance of fish in this estuary. Such a situation would parallel that recorded in the Thames Estuary, in which, in that case, a marked improvement in oxygen concentrations in the 1960s and 1970s, was accompanied by a pronounced increase in fish abundance (Andrews, 1984; Andrews and Rickard, 1980).

The species composition of the fish fauna in the Severn Estuary undergoes consistent cyclical annual changes, which is due in part to the sequential immigration and emigration of marine estuarine-opportunist species during autumn and early winter (Potter et al., 1986, 1997). Variations in the periods when the main fish species attain peak abundance in other holarctic macrotidal estuaries indicate that the ichthyofaunal compositions in those estuaries undergo comparable cyclical changes (e.g. McErlean et al., 1973; Araujo et al., 1998; Maes et al., 1998). However, the recruitment strengths of the different marine estuarine-opportunist species in the Severn and other holarctic estuaries vary markedly between years (Claridge et al., 1986; Elliott et al., 1990; Araujo et al., 1998). In the case of the Severn Estuary, such variability may be due, in part, to inter-annual variations in environmental conditions, e.g. the water temperature and salinity that prevail in the estuary at the time when recruitment typically occurs.

The present study was undertaken firstly to test the hypothesis that the marked improvement that has occurred in the water quality of the Severn Estuary over the last two to three decades will have been accompanied by an increase in the abundance of the main fish species and by a change in the species composition of the ichthyofauna. We thus sampled the Severn Estuary in 1996–1999, using precisely the same methods as those previously employed in 1972–1977, and then compared the data on the fish community in these two periods. Since any intra-annual trends in the overall species composition of the ichthyofauna of the Severn Estuary will reflect, to a large degree, those exhibited by the relative abundances of the most numerous species, we have examined whether such trends are also influenced by those of the suite of least abundant species. Emphasis was then placed on testing the hypothesis that the species compositions and/or abundances of the different main components of the fish fauna, i.e. the marine estuarine opportunist, diadromous and freshwater species, will each exhibit a regular pattern of change during the year and thus collectively contribute to the cyclical changes in composition exhibited by the fauna as a whole throughout the year. Our next aim was to test the hypothesis that, since the marine estuarine opportunist species comprise some species with a more northerly distribution and others with a more southerly distribution, the optimal temperature requirements for spawning will vary amongst those species and, as a consequence, the years of strong and weak recruitment will vary among those species. We have also tested the hypothesis that, since most of the marine estuarine-opportunistic species spawn in the spring and as temperature will almost certainly influence their spawning times (Lam, 1983), the recruitment times of the species into the estuary may be correlated, i.e. if the recruitment of one species occurs later than normal in a year, it will likewise be delayed in other species. Finally, we have determined whether the overall strength and timing of the recruitment of marine estuarine-opportunist species into the estuary are related to salinities and water temperatures in the estuary. To achieve the above aims regarding recruitment, we have developed a new approach for establishing whether or not large sets of correlations amongst times or strengths of recruitment (internal correlations) and between recruitment statistics and environmental variables (cross-correlations) are significant.

2. Materials and methods

2.1. Sampling regime

Fish were collected from the cooling water intake screens of the Oldbury Power Station, which draws water from the inner Severn Estuary (see Fig. 1 in Claridge et al., 1986). Sampling was carried out weekly between early July 1972 and late June 1977 (see Claridge et al., 1986) and in at least 2 weeks in each month between January 1996 and June 1999 except for in July and August 1998. The number of each species in each sample, which represents the catch taken during the previous 24 h, was standardised to a given volume of intake water, i.e. 2.2×10^9 l day^{-1}, the volume which, in 1972/1977, was typically drawn daily through the intake screens in the autumn and early winter, the period of the year when fish abundance was greatest. The numbers of each fish species in each of the four standardised samples in each month from July 1972 to June 1977 were then summed, while those in each of the two or three standardised samples collected in each month from January 1996 to June 1999 were summed and then adjusted so that they corresponded to four samples per month and thus to the same monthly sampling effort as in 1972/1977. The reader is referred to Potter et al. (1997) for a comprehensive description of the sampling locality and regime, and to Claridge et al. (1986) for a list of the common and scientific names of each species caught in the Severn Estuary.

Salinity was measured at the time of sampling, while water temperatures were derived from continuous recordings supplied by Power Station authorities. The mean of each of these variables in each month was then calculated. In our study, the emphasis, in terms of the possible influence of variables, was placed on salinity and water temperature because these two environmental variables are often regarded as having the greatest effect on the abundance of fish in estuaries (e.g. Thiel et al., 1995; Marshall and Elliott, 1998) and each undergoes a marked change in the Severn Estuary during the year (Claridge et al., 1986).

2.2. Comparisons between species compositions in 1972 / 1977 and 1996 / 1999

The mean numbers of each species in each sequential 2-month period, i.e. July–August, September–October, etc., for each year between July 1972 and June 1977 and between July 1996 and June 1998, were fourth-root transformed and ordinated, using the multidimensional scaling techniques in the PRIMER package (Clarke and Warwick, 1994). The fourth-root transformation ensures that the ordination reflects trends in the abundance of all species, rather than simply those of the one or two species that dominate the catch. Prior to ordination, the Bray–Curtis similarity measure was used to produce the association matrix to determine whether each of the different components of the fish fauna contributed to the trends exhibited by the assemblage as a whole. The above ordination procedure was then adopted separately for the suite of least abundant species, i.e. those that contributed $< 10\%$ to the total numbers of fish in all samples, and for the marine estuarine-opportunistic species to determine whether the composition of each of these two categories undergoes cyclical changes each year.

Direct comparisons between the species composition in the period from July 1972 to June 1977 with those from January 1996 to June 1999 are made difficult by the consistent and progressive change undergone by the species composition during the year. To ameliorate this problem, the mean abundances of each species were calculated for successive 2-month periods and then separated into two groups according to the time of year, i.e. July to December and January to June. The mean abundances of all species and of both the marine estuarine opportunist species and least abundant species in each bimonthly period in each 6-month period during each year of sampling in both decades were then fourth-root transformed and subjected to ordination as described earlier. Two-way similarity percentages (SIMPER 2) was employed to determine the species most responsible for any dissimilarities between decades (Platell et al., 1998).

2.3. Recruitment strengths and times of abundant marine species

Correlation analyses have been carried out on data for four ‘response variables’, namely the mean monthly abundances and months of peak abundance of eight major marine estuarine-opportunist species in each of the 5 years between July 1972 and June 1977, and the times between July 1 and when those mean monthly and peak abundances of each of those species were attained. July 1 was chosen as a reference point because the new and strong 0 + age class of the eight selected species had not yet started to enter the estuary and as they each attained peak annual abundance at some time during the ensuing 6 months. Note that the time to peak abundance is a single integer, denoting the month in which the modal abundance is reached, and is likely to contain less detailed information than the continuous variable, time to mean monthly abundance. Note also that these correlation analyses did not include the sand goby and flounder, which are also marine estuarine-opportunist species and numerous in the Severn Estuary, because the first species was shown during the study to comprise two morphologically very similar species (Webb, 1980) and the 0 + age class of the second is relatively abundant in the estuary throughout the year (Claridge et al., 1986; Hardisty and Badsha, 1986).

In our analyses, we have avoided the type of ‘data snooping’ that involves selecting those correlations which, in a wide range of pair-wise comparisons between the abundances of different species and various environmental variables, are significant at the 5% level, and then using those results to draw biological conclusions. The latter procedure is flawed because of the uncontrolled probability of a Type I error, i.e. the chance of deducing a significant result when there are no genuine correlations. Instead, we have calculated the complete set of pair-wise correlations for the selected eight major marine fish species between 1972 and 1977 and performed a single test to determine if the set of correlations departs from that which would be expected by chance. For a single response variable (e.g. peak monthly abundance), the null hypothesis is that there would be no correlation between any of the 28 pairs of species. The 28 correlations are therefore ranked from largest negative to largest positive and plotted against their ranks, producing a 'correlation profile'. Since the number of years involved is small, some correlations might be expected to be close to 1.0 by chance alone, even under the null hypothesis. Departure from the null is then more likely to be detected by a larger than expected number of moderately high correlations.

The correlation profile (CPROF) test performs m simulations (here, $m = 1000$), for each of which the values of the response variable across the 5 years are randomly permuted, independently for each species. The resulting 1000 correlation profiles are averaged to give a simulated mean profile, and a further 1000 random permutations of the data matrix are generated. The absolute difference of each new profile from the simulated mean is recorded in a statistic D, and the departure of the real profile from the simulated mean is then compared with this 'null distribution' of D, as in any randomisation test. The results are displayed by a plot of the real profile contrasted with the mean, upper and lower 5% profiles under the null hypothesis (at any point, 5% of the simulated curves lie above the upper bound, and 5% below the lower bound).

A related display is a 'cross-correlation profile' (CCPROF), correlating every combination of a species with an environmental variable (here eight species and two environmental variables, making 32 cross-correlations). A departure statistic D_c is defined in the same way as for D, except that the randomisations of the five yearly values within each species (and environmental variable) are not performed independently for each variable. More relevant to a null hypothesis of no cross-correlations is a constrained permutation procedure in which a random permutation of the years is chosen but applied to all species in the same way. Similarly, an (independent) random permutation of the years is applied to all environmental variables, as a block, the correlation profile test proceeding as before. Here, there are only a limited number of permutations, and the null distribution is constructed from all possible permutations rather than a random set of simulations.

In spite of the limited time period of this data set, these CPROF and CCPROF routines therefore provide a rigorous test to determine whether there is any evidence of correlation structure. Tests using this approach have clear advantages over a standard Bonferroni procedure, in their power to detect a range of alternative hypotheses. For example, with few years, chance correlations close to 1.0 are possible and a Bonferroni correction (based essentially on the maximum observed correlation) would never result in rejection of the null, even in a case (as here) where departure from the null is indicated by the presence of too many intermediate-sized positive correlations.

3. Results

3.1. Comparisons between the abundances of fish in 1972/1977 and 1996/1998

The number of fish species recorded annually in samples collected from the intake screen of the Oldbury Power Station between July 1972 and June 1977 increased progressively from 42 in 1972/1973 to 48 in 1973/1974 to 53 in 1974/1975 and then to 62 and 63 in 1975/1976 and 1976/1977, respectively (Claridge et al., 1986). Although the 50 and 49 species recorded at Oldbury in July–June of 1996/1997 and

1997/1998, respectively, lie within the range for the above years, it must be borne in mind that the number of 24-h samples collected monthly in 1996/1998 were less than in 1972/1977, i.e. 2 or 3 vs. 4 (see Section 2). The only species that was recorded in 1996/1999 and not in 1972/1977 was the zander or pike perch (*Stizostedion lucioperca*). This teleost, which is a valuable freshwater sporting fish and native to eastern Europe, has been introduced into open waterways in England at intervals since the late 1800s (Wheeler, 1969) and, from the results of the present study, has now established itself in the catchment of the River Severn.

The total number of fish, after standardising the abundances to a constant intake volume for each sample and to four samples per month (see Section 2), rose progressively and by ca. 5.3 times from 8740 fish in 1972/1973 to 45,987 in 1975/1976 and remained at more than 40,000 fish in 1976/1977 (Claridge et al., 1986). The mean annual number of fish in 1972/1977, i.e. 29,366, is far lower than the mean annual number for 1996/1998, i.e. 95,828 (Table 1). Furthermore, the two annual values for the latter period are over 1.4 and 2.7 times greater, respectively, than even the maximum annual values recorded during the 5 years in the 1970s (Table 1). Moreover, the minimum number of fish recorded for the January to June periods in the 4 years in the 1990s for which there are data, i.e. 1996–1999, exceeded the maximum recorded during the same period in any of the 5 years in the middle 1970s.

The greater number of fish caught per annum in the 1996/1998 than 1972/1977 periods can be attributed largely to far higher catches of sand goby, whiting, bass, thin-lipped grey mullet, herring, sprat, Norway pout and Dover sole (Table 1). Indeed, the annual numbers of each of these species were between 2.1 and 61.3 times greater in 1996/1998 than in 1972/1977 and, in the case of sand goby, sprat and Norway pout, the least of the two annual catches in 1996/1998 was greater than the maximum annual catch recorded in 1972/1977. In contrast to the situation with the above six species, the mean annual abundances of poor cod, River lamprey and flounder were lower in 1996/1998 than 1972/1977, the differences corresponding to factors of 24.2, 1.8 and 1.5, respectively, while those of sea snail, twaite shad, eel, three-spined stickleback, bib and common goby differed by factors of less than 1.5 times between the two decades (Table 1).

In terms of their relative abundance, bass increased in rank from 4 to 2, sprat from 11 to 4, Dover sole from 17 to 12 and Norway pout from 20 to 5, while flounder declined from 3 to 7, sea snail from 5 to 8, poor cod from 6 to 17 and twaite shad from 8 to 11 (Table 1). The rankings of species such as sand goby, whiting, thin-lipped grey mullet, eel, herring, bib and common goby remained either the same or differed by only one between the two decades. In terms of percentage contributions to the total catch, the mean overall values for sand goby, bass, sprat and Norway pout were appreciably greater in 1996/1998 than in 1972/1977, whereas the reverse was true for whiting, flounder, sea snail and poor cod (Table 1).

3.2. Comparisons between the species compositions in 1972/1977 and 1996/1998

When the mean of the transformed abundances of each fish species in the samples obtained for each bimonthly period between July and June in each of the 5 years

Table 1

Ranks, mean annual abundances, percentage contributions and minimum and maximum abundances of the most abundant species of fish collected at Oldbury in the 5 years between July 1972 and June 1977 and in the 2 years between July 1996 and June 1998, and the proportional difference between the mean abundances in the former and latter periods

Species name	Common name	1972/1977					1996/1998					Difference
		Rank	Mean	%	Min.	Max.	Rank	Mean	%	Min.	Max.	
Pomatoschistus minutus complex	Sand goby	1	8572	29.2	2232	12,521	1	36,129	37.7	24,784	47,474	+ 4.2
Merlangius merlangus	Whiting	2	8294	28.2	164	15,911	3	17,714	18.5	15,878	19,550	+ 2.1
Platichthys flesus	Flounder	3	2896	9.9	1825	5471	7	1899	2.0	1135	2662	− 1.5
Dicentrarchus labrax	Bass	4	2156	7.3	82	8896	2	22,585	23.6	5943	39226	+ 10.5
Liparis liparis	Sea snail	5	1980	6.7	509	5045	8	1466	1.5	814	2117	− 1.4
Trisopterus minutus	Poor cod	6	846	2.9	154	2712	17	35	< 0.1	15	55	− 24.2
Liza ramada	Thin-lipped grey mullet	7	779	2.7	38	3348	6	2477	2.6	570	4384	+ 3.2
Alosa fallax	Twaite shad	8	776	2.6	73	1790	11	729	0.8	44	1413	− 1.1
Anguilla anguilla	Eel	9	737	2.5	529	943	10	949	1.0	930	967	+ 1.3
Clupea harengus	Herring	10	574	2.0	54	1396	9	1444	1.5	1313	1574	+ 2.5
Sprattus sprattus	Sprat	11	360	1.2	35	614	4	5402	5.6	4286	6571	+ 15.0
Gasterosteus aculeatus	Three-spined stickleback	12	254	0.9	58	621	14	178	0.2	132	223	+ 1.4
Lampetra fluviatilis	River lamprey	13	191	0.7	80	381	16	109	0.1	51	166	− 1.8
Trisopterus luscus	Bib	14	182	0.6	6	422	13	184	0.2	125	243	0
Pomatoschistus microps	Common goby	15	149	0.5	1	350	15	159	0.2	115	202	+ 1.1
Trisopterus esmarkii	Norway pout	20	48	0.2	24	78	5	2944	3.1	224	5663	+ 61.3
Solea solea	Dover sole	17	75	0.3	40	122	12	345	0.4	311	378	+ 4.6
Total (all species)			29366		8740	45987		95828		65088	124396	

Annual abundances represent the sum of the number of fish in four 24-h samples per month after those numbers had been adjusted to the same sampling effort (see Section 2).

between July 1972 and June 1977 and between July 1996 and June 1998 were subjected to ordination, the points for the bimonthly data in both decades pursued a similar consistent and very pronounced anticlockwise direction on the ordination plot (Fig. 1a). However, the points for each bimonthly period in the 1970s lay to the left of those for each of the corresponding bimonthly periods in the 1990s. When the bimonthly data for the numbers of the least abundant species, i.e. those that never contributed more than 10% to the total numbers of fish in any bimonthly period, were similarly pooled and subjected to ordination, the points for these data in both periods also each followed the same pronounced cyclical pattern of change and those for the 1970s also lay to the left of those for the corresponding bimonthly periods in the 1990s (Fig. 1b).

The points for the samples of the marine estuarine-opportunist species followed very similar trends to those for the whole fish fauna in the corresponding periods in both decades (cf. Figs. 1a and 2a). The superimposition of the relative abundances of marine

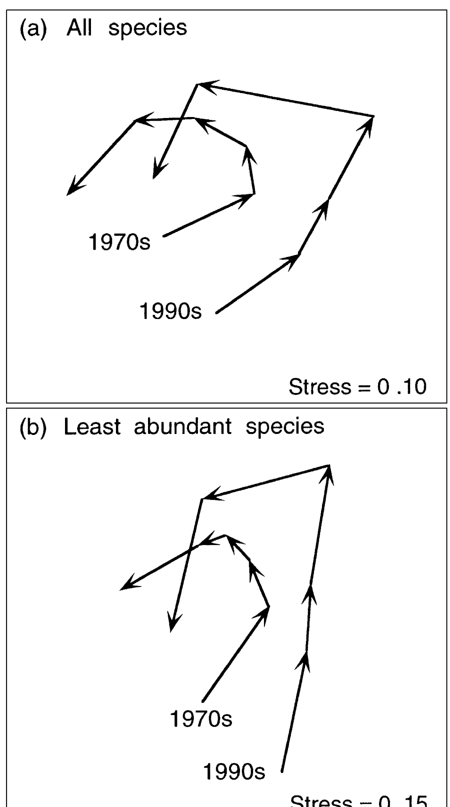

Fig. 1. Non-metric multidimensional scaling (MDS) ordination of the abundances of (a) all species and (b) the suite of least abundant species in samples of fish collected from Oldbury in the Severn Estuary in sequential bimonthly periods (i.e. July and August, September and October, etc.) between July and June of 1972 to 1977 and 1996 to 1998. N.B. In this figure and in Fig. 2, data for each of the corresponding bimonthly periods in each decade have been pooled.

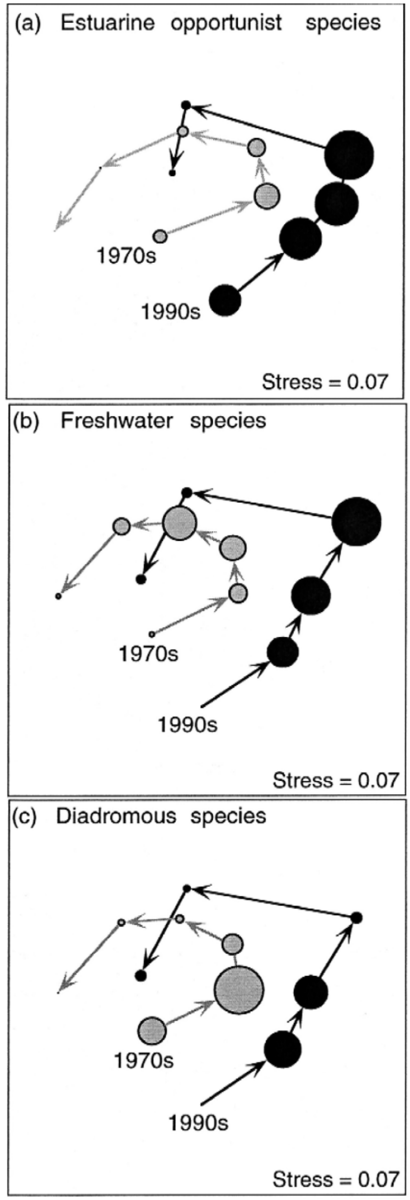

Fig. 2. (a) MDS ordination of the abundances of marine estuarine-opportunist species in samples of fish collected from Oldbury in the Severn Estuary in sequential bimonthly periods (i.e. July and August, September and October, etc.) between July and June of 1972 to 1977 and 1996 to 1998. The sizes of the circles superimposed on the points in the ordination plot for the numerous marine species are directly proportional to the root root abundances used for the ordination. The relative abundances of freshwater (a) and diadromous species (b) are likewise denoted by the size of the superimposed points on the ordination plot for all species (see Section 3).

estuarine-opportunists on this ordination plot demonstrate that in 1972/1977 the relative overall abundance of this category increased progressively between July/August and September/October, reflecting the influx of large numbers of their juveniles (Claridge et al., 1986), and then declined progressively in the subsequent 6 months (Fig. 2a). While the trends were similar in 1996/1998, the abundances in this year were greater and peaked slightly later. The relatively greater abundance of estuarine-opportunists in the September to December period of 1996/1998 than of 1972/1977 was mainly due to the immigration of far greater numbers of species such as the sand goby, whiting, bass and thin-lipped grey mullet.

Since the freshwater and diadromous categories were often represented in samples by only a small number of species and, on occasions, were not even caught, it was inappropriate to subject the abundances of the species in these two categories to ordination. However, the superimposition of the relative abundance of freshwater species on the ordination plot for all species in 1972/1977 and 1996/1998 showed that, in both decades, the overall numbers of this category increased progressively between July/August and either January/February or November/December, when freshwater discharge was increasing and salinities were thus decreasing, and that they subsequently declined progressively in March/April and May/June, as freshwater discharge decreased and salinity increased (Figs. 2b and 4). Furthermore, superimposition of the relative abundance of diadromous species on the ordination plot for all species demonstrated that the relative abundances of these species followed similar trends in the two periods, peaking in September/October or November/December, and then declining progressively during the subsequent bimonthly periods (Fig. 2c).

When the abundances for all species in each bimonthly period between July and December of each year were subjected to ordination, the three bimonthly points for that 6 months in both decades followed a similar sequential progression from left to right across the ordination plot (Fig. 3a). However, all of the points for each of the bimonthly periods in 1996, 1997 and 1998 lay below and/or to the right of those for each of the corresponding bimonthly periods in each of the 5 years from 1972/1973 to 1976/1977 (Fig. 3a). The above trends were paralleled by those for the bimonthly periods in January to June in both of these decades, except that, in this case, the points for the 1990s lay below and/or to the left of those for the 1970s (Fig. 3d). The above differences between the locations of the points on the ordination plots for the whole fish fauna in the bimonthly periods in both July to December and January to June in 1972/1977 and 1996/1999 were largely mirrored by those for both the marine estuarine-opportunist species (Fig. 3b,e) and the least abundant species during the same time periods (Fig. 3c,f).

SIMPER 2 demonstrated that the fish fauna in July to December in 1996–1998 was distinguished from that of the corresponding 6 months in 1972 to 1976 by relatively greater abundances of bass, sand goby, whiting, herring, thin-lipped grey mullet, cod and sand smelt. In the January to June period, the samples in 1996 to 1999 contained relatively greater numbers of bass, whiting, herring, conger eel and thin-lipped grey mullet and relatively lower abundances of poor cod and flounder. In the case of the least abundant species, July to December in 1996 to 1998 was characterised by relatively greater contributions of carp, lumpsucker, scaldfish and mackerel. Between January and

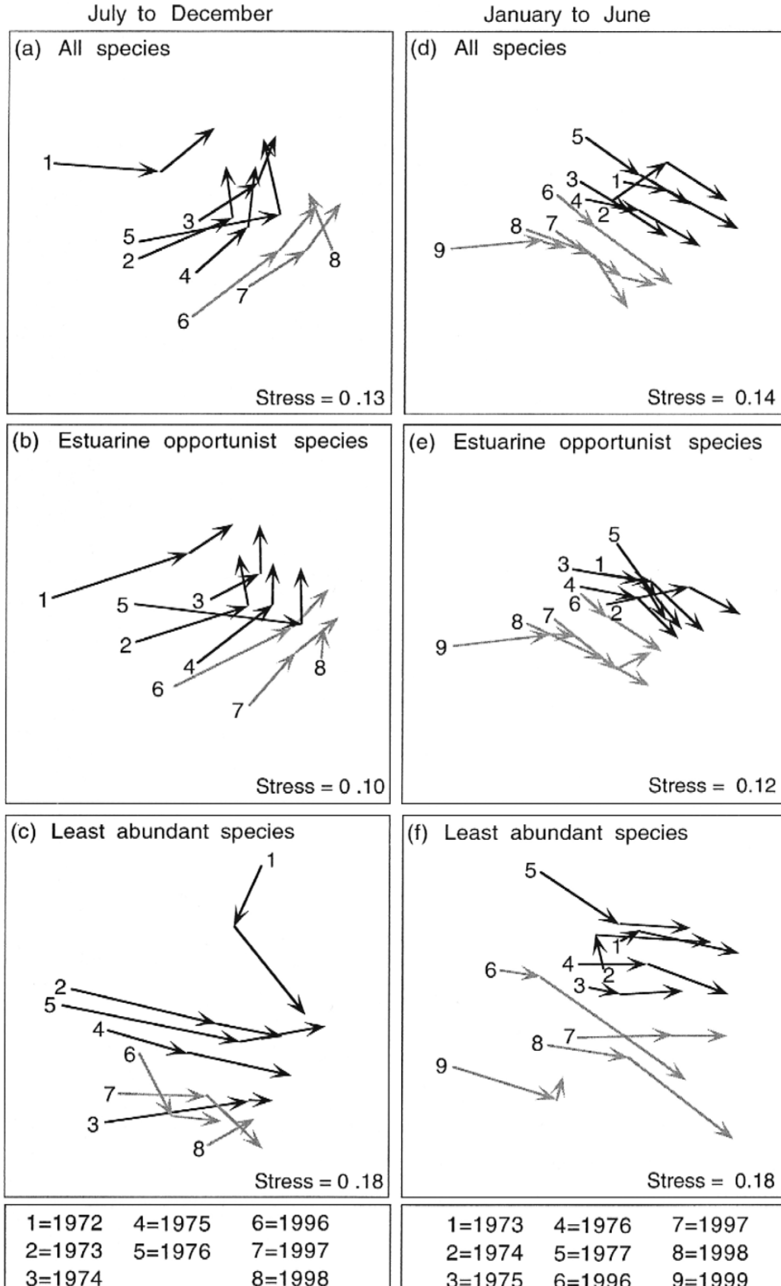

Fig. 3. MDS ordination of the abundances of all species, marine estuarine-opportunist species and the least abundant species in samples of fish collected from Oldbury in the Severn Estuary in sequential bimonthly periods between July and December in 1972 to 1977 and 1996 to 1998 (a–c) and between January and June (d–f) in 1972–1977 and 1996–1999.

June, the 1972 to 1977 years were characterised by relatively greater contributions of cod, haddock and sea lamprey, whereas the 1996 to 1999 years were characterised by greater contributions of scaldfish, roach and five-bearded rockling.

3.3. Annual recruitment strengths of main species in 1972/1977

The years between July 1972 and June 1977 in which the abundances of the eight most numerous marine estuarine-opportunist fish species (but excluding the sand goby complex and flounder—for rationale see Section 2) attained their monthly maxima were not always the same (Fig. 4). Thus, maxima were attained by sprat and herring in 1973/1974, by bib and sea snail in 1974/1975, by poor cod in 1975/1976, and by bass, whiting and thin-lipped grey mullet in 1976/1977. The maximum monthly abundances of the above eight species in any year ranged from 244 for bib in September 1974 to 5718 for whiting in October 1976/1977 (Fig. 4). The peak annual values for the abundance of whiting rose progressively in each of the 5 years of the study, whereas that of sprat declined progressively between 1973/1974 and 1976/1977. However, such sequential trends were not observed with any of the other six marine estuarine-opportunist species. The maximum and minimum annual peak abundances over the 5 years differed by a factor of between about 10 and 18 times in the cases of sea snail, poor cod and sprat, and by between approximately 70 and 110 times with whiting, bass, thin-lipped grey mullet and herring (Table 1).

3.4. Correlations among the recruitment patterns of species and environmental variables

Correlation profile analysis demonstrated that, during the 5 years between July 1972 and June 1977, the mean monthly abundances of sprat, herring, bass, poor cod, bib, whiting, thin-lipped grey mullet and sea snail were not correlated ($p = 0.59$). This point is emphasised by the fact that the departure statistic (D) was only 0.08 and that the "real" correlation profile is close to the "simulated mean" profile and, throughout its range, is positioned below the upper boundary of the profile for the 95% confidence bound (Fig. 5a). The above lack of correlation was paralleled by the situation with the peak monthly abundances of the above eight species over the 5-year period, for which the departure statistic was even smaller ($D = 0.05$ and $p = 0.95$, data not presented). In contrast, there was a significant relationship ($p < 0.01$) between the time of mean monthly abundance amongst the eight species over the 5 years. The departure value was relatively high ($D = 0.33$) and the real correlation profile is typically positioned above the upper 95% bound (Fig. 5b). Furthermore, the times to modal (peak) abundance for those species were also strongly correlated ($D = 0.29$, $p < 0.01$, data not presented). Note that with this direct interpretation of D, when all observed correlations are greater than expected, the average correlation from this set is 0.29 higher than would be expected by chance (i.e. approximately zero) when there are no genuine associations. The above results imply that when, in any given year, one species takes a longer or shorter than normal time to reach their mean monthly and peak values in abundance,

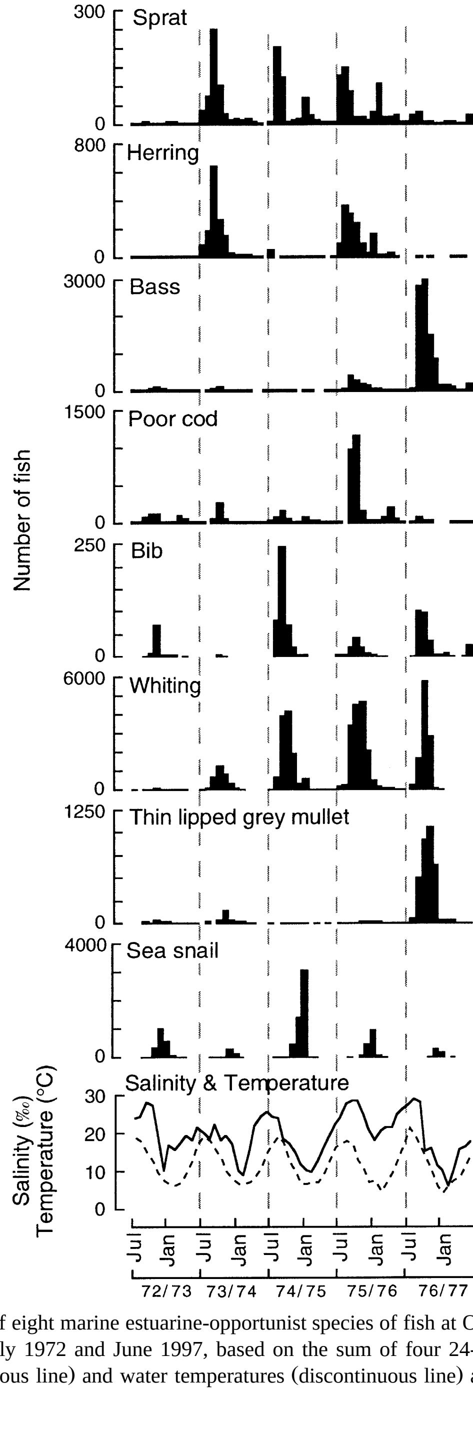

Fig. 4. Monthly numbers of eight marine estuarine-opportunist species of fish at Oldbury in the Severn Estuary in each month between July 1972 and June 1997, based on the sum of four 24-h samples per month. Mean monthly salinities (continuous line) and water temperatures (discontinuous line) are also shown.

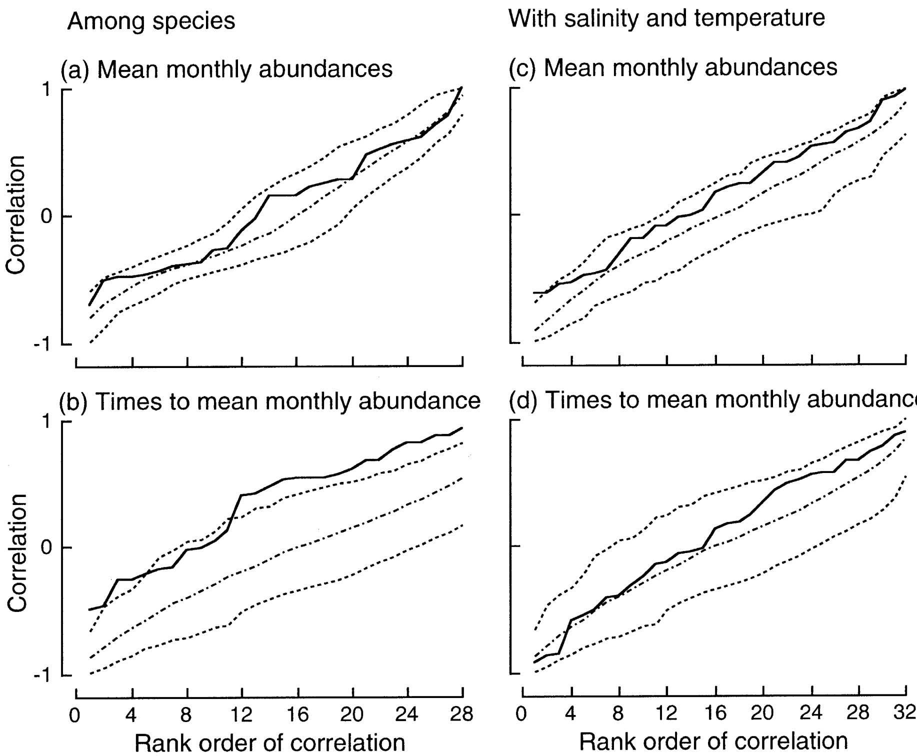

Fig. 5. Correlation profile analyses for mean monthly abundances (a) and (c) and times from July 1 to mean monthly abundance (b) and (d). (a) and (b) represent all pairwise correlations between the eight species investigated and (c) and (d) the cross-correlations between the eight species and the four environmental variables (salinity and water temperature in both July/August and September/October). The continuous line denotes real correlations, ranked from smallest to largest, contrasted with the mean simulated profile (broken line) under the null hypothesis of absence of genuine correlations. The dashed lines indicate upper and lower bounds for a single simulated profile (see text).

other species will likewise take a longer or shorter time, respectively, to achieve those values.

Having established that the time of peak abundance of the eight species is positively correlated, it becomes legitimate to explore in detail which species pairs are most closely associated in this respect. The maximum correlation coefficients were between bass, poor cod, bib and whiting, with three of these six inter-correlations being in excess of 0.85. Sprat is also positively associated within the members of this group (correlations from 0.55 to 0.81) and with herring (0.81). These inter-relationships in year-to-year fluctuations in the timing of recruitment can again be summarised by clustering and ordination. The appropriate dissimilarity matrix is not now Bray–Curtis but the normalised Euclidean distance (Clarke and Warwick, 1994), leading to the non-metric MDS plot shown in Fig. 6. The interpretation here is that species that lie close together on the plot have matching year-to-year fluctuations in their recruitment times. The analysis

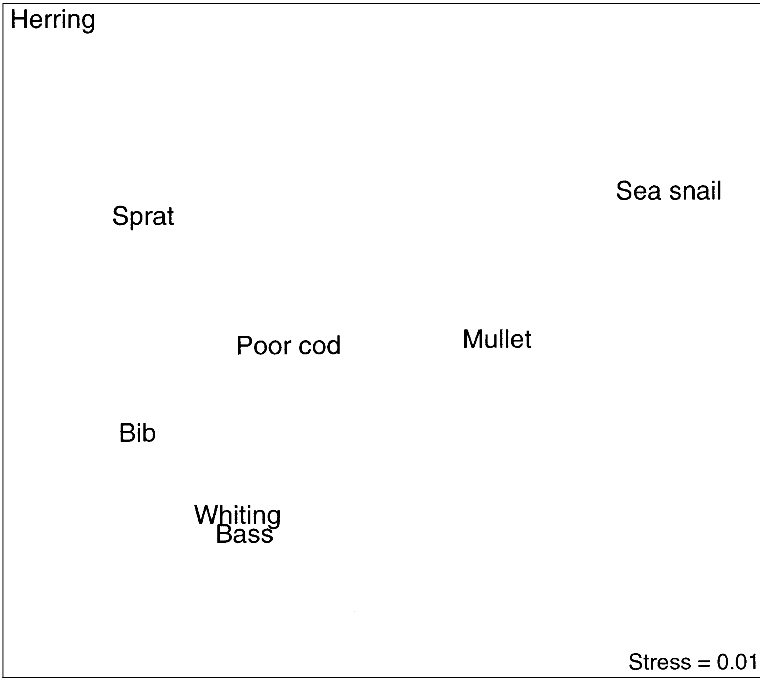

Fig. 6. MDS configuration for the eight species used in correlation profile analysis, based on time to mean monthly abundance for the 5 years 1972/77 and using normalised Euclidean distance as the dissimilarity measure.

removes any direct effect of differences between each pair of species in their average time of mean abundance, by examining only whether departures from the average recruitment times are of the same magnitude and direction over the 5 years. Nonetheless, the MDS plot in Fig. 6 shows that the species whose recruitment fluctuations are most highly correlated are those whose average times of mean (or peak) monthly abundances are similar (cf. Figs. 4 and 6). Thus, bass, whiting, bib and poor cod, which tend to reach peak abundance in September and October, form a group in the bottom left hand of the plot below and, in three cases, also to the right of those of herring and sprat, whose abundances peak earlier, i.e. August or September, and below and to the left of those of thin-lipped grey mullet and sea snail, which attain their peak abundances later, i.e. November–January (Fig. 6).

Having determined that there were significant relationships in the timing of recruitment, it was then appropriate to examine whether they had a simple association with year-to-year fluctuations in salinity and temperature within the estuary. When the recruitment strengths and times were cross-correlated with the mean values for salinity and water temperature in the estuary in both July/August and September/October, neither the mean monthly abundances ($p = 0.38$) nor the times to mean monthly abundance ($p = 0.69$) were correlated with these environmental variables. This point is illustrated by the fact that the real correlation profile for the mean abundance and the time to mean abundance was located close to the corresponding simulated mean profile ($D = 0.14$ and 0.11, respectively) and below the upper 95% bound (Fig. 5c and d). The above result was mirrored by the peak monthly abundances, and the times to peak abundance ($D = 0.10$, $p = 0.55$ and $D = 0.05$, $p = 0.99$, respectively). Furthermore, essentially the same results were obtained when salinity and water temperature were treated separately. The cross-correlation profile analysis indicates that there were no such correlations, over and beyond those that would be expected by chance.

4. Discussion

4.1. Long-term changes in species abundance and composition

The results of the present study demonstrate that, on the basis of the same sampling regime, the abundance of fish at Oldbury in the Severn Estuary increased markedly between July 1972–June 1977 and January 1996–July 1999. The substantial increase in fish abundance in the 1990s reflected, in particular, marked increases in the numbers of sand goby, whiting, bass, thin-lipped grey mullet, herring, sprat and Norway pout. Amongst these seven species, the Severn Estuary is located towards the northern limit of the distribution of bass and thin-lipped grey mullet and towards the southern limit of Norway pout and well within the main body of the range of the other species (Wheeler, 1969).

The increases in the numbers of the above major contributors to the ichthyofauna of the Severn Estuary provide strong circumstantial evidence that conditions for successful spawning, larval survival and/or recruitment of these marine estuarine-opportunist species have improved over the last two to three decades. Although the conditions for spawning in the Bristol Channel may have improved during this period, any changes in that vast water body are likely to have been much less pronounced than in the far more restricted confines of the Severn Estuary, into which particularly large volumes of industrial and domestic waste used to be discharged (Martin et al., 1997; Anon, 1999). Certainly, it is now well established that the imposition of much stricter regulations on the discharge of heavy metals and organic waste has resulted in a marked improvement in the water quality of this estuary over the last two to three decades (Little and Smith, 1994; Vale and Harrison, 1994; Anon, 1997, 1999; Martin et al., 1997). The fact that the overall abundance of fish rose during the 1970s (Claridge et al., 1986) suggests that the fish fauna had already begun to respond to the improvement that was occurring in environmental conditions during that period.

The increase in overall abundance of fish in the Severn Estuary during the last 20–30 years parallels that recorded in the Thames Estuary between the 1960s and 1970s (Thomas, 1998). In the case of the Thames Estuary, the increases in the abundance (and also diversity) of fish was attributable, in particular, to an improvement in the levels of dissolved oxygen, as a result of a marked reduction in sewage effluent (Thomas, 1998). However, since the Severn Estuary has always been well mixed, and thus well oxygenated, the causal factor(s) that led to an increase in fish abundance in this estuary are unlikely to have been the same as in the Thames Estuary. It thus seems relevant that discharges of industrial effluents, including cadmium, a particularly toxic element, have declined markedly in the Severn Estuary during the last 20–30 years (Little and Smith, 1994; Vale and Harrison, 1994; Anon, 1997, 1999; Martin et al., 1997). The increases in fish abundance in the Severn Estuary during these years may therefore, at least partly, have resulted from fish no longer being exposed to exceptionally high levels of deleterious contaminants and which previously would have been likely to have had sublethal effects and thereby reduced the 'fitness' of members of the fish assemblage.

Although the abundance of the seven species mentioned earlier increased markedly between 1972/1977 and 1996/1998, those of flounder and sea snail, which are also relatively abundant in the Severn Estuary, underwent modest declines of 1.5 and 1.4 times, respectively, while that of poor cod decreased dramatically. Thus, although the major species in the ichthyofauna of the Severn Estuary were almost invariably the same in 1996/1999 as in 1972/1977, the relative contributions of the various species changed between these two decades. This strong implication that the composition of the fish fauna changed between the 1970s and 1990s is supported by the fact that, on the ordination plot that utilise the abundance data for each corresponding bimonthly period in each decade, the points for the years 1996/1998 lay to the right of those for the years 1972/1977 (Fig. 1a). This accounts for the fact that, when the data for the total fish fauna in each bimonthly period in each July to December period of 1996–1998 and in each January to June period in 1996 to 1999 were treated individually, the points for the two decades on the ordination plot were discrete (Fig. 3a,d). The fact that the trends exhibited by the marine estuarine-opportunists paralleled closely those of the total fauna (cf. Figs. 3a,b,d,e and 2a) emphasises the important contribution made by these marine species to the ichthyofauna of the Severn Estuary. However, since similar results were produced by ordination, when the data were restricted to the less abundant species (Figs. 1b and 3c,f), the shift in the composition of even these species also contributed to the overall change in species composition between the 1970s and 1990s.

While the abundance of poor cod declined dramatically between the 1970s and 1990s, the congeneric and behaviourally similar Norway pout underwent the greatest relative increase in abundance of all species in the second decade. The decline in flounder in the Severn Estuary parallels that recorded in the Thames Estuary, in which the decline was attributed to increased predation of the 0 + year class (Thomas, 1998). The decline in the numbers of the River lamprey is consistent with reports that, in UK, the abundance of this anadromous species has been declining for several years (e.g. Maitland and Lyle, 1990) and which, as a consequence, has led to it being listed in the 1996 IUCN Red List of threatened animals compiled by the World Conservation Monitoring Centre. The decline in the abundance of the River lamprey is presumably due to the impediments posed to the upstream migration of the adults by the construction of weirs and dams and/or to deleterious changes to the silt habitats of the larvae.

4.2. Seasonal cycling in species composition

Our data show that, during both the 1970s and 1990s, the compositions of the suites of both the marine estuarine-opportunist and less abundant species each exhibited the same type of pronounced annual cyclical changes in the Severn Estuary. Furthermore, the overall abundances of both the freshwater and diadromous categories also underwent a pronounced cyclical change during the year. In the case of the marine estuarine-opportunist species, the overall abundance and prevalence were typically highest in autumn and early winter, when the new 0 + recruits of marine estuarine-opportunists typically enter the estuary. Freshwater species were either absent or in very low numbers in summer and early autumn, when salinities were at their highest, and relatively higher in winter, when salinities were at their lowest, while diadromous species were most abundant during autumn. However, it should be recognised that the different species within each life cycle category often attain peak abundances at rather different times. This accounts for the highly consistent and regular pattern of change that is undergone throughout the year by the overall composition of the ichthyofauna. Our data thus now demonstrate that the cyclical change undergone annually by the composition of the fish community of the Severn Estuary reflects the cumulative effect of the time-staggered and usually unimodal abundance patterns exhibited by the various species within each life cycle category.

4.3. The strengths and timing of recruitment of marine species

The use of correlation profile analyses has shown that there was no significant intercorrelation between the annual trends in the relative abundances of eight numerous marine estuarine-opportunist species in the inner Severn Estuary. These results are consistent with the observation that, although the abundances of groups of two or three species sometimes exhibited their annual maxima in the same year, the trends exhibited annually by the peak abundance of any one species during the five years were not necessarily paralleled by those of any other species (Fig. 4). Furthermore, cross-correlation profile analyses demonstrated that the recruitment strengths of those eight species were related neither to the salinity nor the water temperature in the inner Severn Estuary, nor to a combination of these variables. Our confidence that the types of tests we have developed were sufficiently sensitive to reveal significant correlations is supported by the ability of these tests to reveal significant correlations between the timing of the immigrations of different species in the different years, even though such interannual variations were only of the order of 2–3 weeks.

The results of the tests employed in this study suggest that it is inappropriate to conclude that, in any given year, a strong recruitment by two or more of the eight species into the inner Severn Estuary is due to anything other than chance. In other words, the factors that lead to the strong recruitment of one species into that region are not necessarily the same as those that would result in the strong recruitment of another species in the same year. Indeed, there were numerous examples in which two species were very abundant in a year, and yet in other years, one of those species was abundant whilst the other was poorly represented. For example, the maximum monthly abundances of whiting in the inner Severn Estuary in 1974/1975, 1975/1976 and 1976/1977 were very high, ranging from 4160 to 5178 fish, whereas those of thin-lipped grey mullet, while also relatively high for that species in 1976/1977, i.e. 1054 fish, were very low in 1974/1975 and 1975/1976, i.e. 13 and 32 fish respectively. It is therefore not surprising that the level of recruitment of those marine species into their estuarine nursery areas reflects neither the salinity nor water temperature in those waters. However, the relative abundances of certain fish species do change along the length of the estuary, presumably in response, at least in part, to the presence of a salinity gradient (Henderson, 1989; Elliott et al., 1990; Marshall and Elliott, 1998).

In contrast to the non-significant correlations found between the mean or peak abundances of the eight marine estuarine-opportunist species over the 5 years, the correlation profile analysis provides clear evidence that the timing of the recruitment of those species was associated. Thus, for time to both mean abundance and peak abundance, the correlations between species are, on average, 0.3 higher than would be expected by chance and the data in Fig. 5b show that at least half of the correlations exceed those that would be expected from the null hypothesis. Note also that there is no excess of negative correlations, implying that a shift in the timing of recruitment of one marine species into its estuarine nursery habitat was accompanied by a shift in the same direction in the timing of the recruitment of the other species into the same region, and that such shifts were most highly correlated in the case of species that tended to enter the estuary at a similar time of the year. This latter finding is consistent with the fact that the timing of movements into the estuary are more likely to be linked to a common influence outside the estuary, when that recruitment takes place during similar rather than different periods. However, shifts in the time of mean and peak abundances of those species were correlated neither with the salinity nor water temperature within the estuary nor with a combination of those two variables.

From the above, it follows that the recruitment times of the 0 + age class of these marine species are more likely to be influenced by environmental conditions outside than inside the Severn Estuary. Since there is strong circumstantial evidence that most marine estuarine-opportunist species spawn in the nearby Bristol Channel into which the Severn Estuary discharges (Russell, 1980; Claridge et al., 1986), the timing of the recruitment of these species into their estuarine nursery area is likely to be influenced by variations in environmental conditions in the spawning area and their effect on spawning time, and/or by annual fluctuations in the characteristics of the currents that transport their larvae and juveniles towards the estuary.

Although the use of internal and cross-correlations failed to detect significant relationships between either the annual abundances of different marine species in the inner Severn Estuary or between those abundances and either salinity or water temperature in that region, the interannual variations in abundances of certain species in a region just outside the Severn Estuary have been found to be significantly correlated with environmental variables (e.g. Henderson and Holmes, 1991; Henderson and Seaby, 1994). While such correlations may sometimes be biologically valid, it must be borne in mind that attempts to correlate the individual abundances of each of a suite of fish species with a number of environmental variables will be likely to produce some correlations that are significant purely by chance. There thus appears to be a strong case in such studies to use initially the global tests of internal and cross-correlations, developed during the present study, to determine whether it is subsequently justifiable to explore individual correlations. Correlation profile analyses would thus act in the same way as F tests in the analysis of variance, by providing a ‘red light’ to further analyses and interpretation when the global hypothesis of an absence of correlation structure is not rejected. Of course, it should not be overlooked that, where feasible, a more reliable way to avoid the dangers of 'data snooping' is to design the collection of data and experimentation around tightly defined hypotheses involving specified variables. With this approach, only a very few hypothesis tests need to be performed.

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