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Factors influencing the characteristics of the fish faunas in offshore, deeper waters of permanently-open, seasonally-open and normally-closed estuaries

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A B S T R A C T

This study explored the ways in which various factors influence the species compositions, species richness and catch rates of fishes in offshore, deeper waters of the basin and river regions of five estuaries, which are located along ca 400 km of the southern coastline of Western Australia and differ markedly in their physico-chemical characteristics. Gill netting seasonally for two years at sites in the basin and saline lower reaches of the main tributary of the seasonally-open Broke, Irwin and Wilson inlets, the permanently-open Oyster Harbour and the normally-closed Wellstead Estuary yielded 22,329 fishes representing 58 species. Overall, and irrespective of estuary type, the species compositions of the basins and rivers differed markedly. This was attributable to consistently greater abundances of *Mugil cephalus*, and usually also of *Acanthopagrus butcheri*, in the rivers of each estuary and to the restriction of a range of species largely to the basins. However, the compositions in the basins of the five estuaries varied markedly, reflecting differences in the extent and duration of the opening of the estuary mouth and/or whether extensive growths of macrophytes were present. Changes in the ichthyofaunal composition of the normally-closed Wellstead Estuary between the first and second years of the study were attributable, in particular, to the movement of two mugilid species into offshore waters as they increased in size. Cyclical changes in ichthyofaunal composition were conspicuous in both regions of the estuary that underwent the most pronounced seasonal variations in environmental conditions. In each estuary, species richness was greater in the basin than river, where salinities were more variable and fell to lower levels and were thus less conducive to the immigration of most marine species. Catch rates were least in Broke Inlet, which had the lowest primary productivity, and were particularly high in Wellstead Estuary, which is highly eutrophic. The results of this study emphasise that ichthyofaunal composition can vary greatly with region (basin vs river) in microtidal estuaries, a finding that is of direct relevance to managers as these systems are becoming increasingly degraded and yet still constitute important nursery areas for certain fish species and often support recreational and commercial fisheries.

1. Introduction

The estuaries of southern Australia and southern Africa, which are located in microtidal regions, typically comprise a narrow and short entrance channel, a wide central basin area and the saline lower reaches of their tributary rivers (Day, 1981; Bird, 1984; Hodgkin and Hesp, 1998). Sand bars form at the mouths of some of these estuaries and thus prevent exchange between the estuary and the ocean (Jennings and Bird, 1967; Hodgkin and Lenanton, 1981; Cooper, 2001). Although a few estuaries on the south coast of Western Australia remain permanently open, the others either open seasonally or are normally closed (Hodgkin and Hesp, 1998; Potter and Hyndes, 1999). The estuaries on this coast have become variably eutrophic through the input of nutrients from surrounding agricultural land and/or markedly hypersaline through increases in salt runoff from cleared areas (Pen, 1999; Radke et al., 2004; Chuwen et al., 2007). The salinities in some of these estuaries have become so extreme that they have led, at times, to substantial fish mortalities (Young and Potter, 2002; Hoeksema et al., 2006).

As in temperate regions of the northern hemisphere (Haedrich and Hall, 1976; Elliott et al., 2007; Franco et al., 2008), the fish faunas of estuaries in the southern hemisphere contain substantial numbers of marine species that either use these estuaries typically as nursery areas or enter them infrequently as either juveniles or adults and generally in low numbers (e.g. Blaber, 1980; Bennett, 1989; Potter et al., 1993; Potter and Hyndes, 1994, 1999; Whitfield, 1999). However, in contrast to macrotidal estuaries in the northern hemisphere, those of south-western Australia contain several species whose individuals complete their life cycles within these

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systems (Potter et al., 1990; Potter and Hyndes, 1999), an ability that is particularly valuable to species in normally-closed estuaries (Bennett, 1989; Whitfield, 1999; Young and Potter, 2002). Work in southern Africa has shown that the species compositions of the fish faunas in nearshore waters along a coast, where estuaries range from permanently open to normally closed, were related to the duration that each estuary was open to the sea (Bennett, 1989; Vorwerk et al., 2003). Furthermore, the ichthyofaunal composition of an estuary that has been closed for a protracted period can change markedly when the bar at the estuary mouth is breached and thus allows the immigration of substantial numbers of marine species (Young and Potter, 2002; James et al., 2008).

The ichthyofaunal composition of estuaries can vary among years through, in particular, variations in the abundances of those marine species that use estuaries as nursery areas. Such interannual variations can result from interspecific differences in recruitment success among years or periods (e.g. Potter et al., 1997, 2001; Maes et al., 2005) or differences in the degree of access to the estuary among years, through variations in the size and duration of the opening of the estuary mouth in the case of seasonally-open or normally-closed estuaries (Young and Potter, 2002; James et al., 2008). Furthermore, the compositions of the fish faunas of nearshore waters in any given region of microtidal and macrotidal estuaries often undergo seasonal cyclical changes due to time-staggered immigrations and emigrations of certain species (e.g. Claridge et al., 1986; Potter et al., 1986; Young and Potter, 2003a; Maes et al., 2005; Hoeksema and Potter, 2006).

The fish faunas of nearshore, shallow waters of south-western Australian and southern African estuaries, which are usually sampled with seine nets, are dominated by the juveniles of marine species and by small estuarine species (Bennett, 1989; Potter and Hyndes, 1999; Whitfield, 1999; Hoeksema and Potter, 2006; James et al., 2008). In contrast, the ichthyofaunas of offshore, deeper waters, which are frequently sampled by gill netting, contain substantial numbers of larger fishes, which, in south-western Australia, include the adults of estuarine-spawning species, such as the sparid *Acanthopagrus butcheri* and the plotosid *Cnidoglanis macrocephalus*, and the larger juveniles of the marine-spawning mugilids *Aldrichetta forsteri* and *Mugil cephalus* (e.g. Loneragan et al., 1989; Potter et al., 1993; Young and Potter, 2002). Studies on the large permanently-open estuaries on the lower west coast of south-western Australia demonstrate that the compositions of the ichthyofaunas of the main regions of those estuaries differ, reflecting differences in the regions typically occupied by certain species in those systems (Loneragan et al., 1987, 1989; Loneragan and Potter, 1990).

Representative samples of fishes have been obtained from the seasonally-open Broke, Irwin and Wilson inlets, the permanently-open Oyster Harbour and the normally-closed Wellstead Estuary, which are located along ca 400 km of the south coast of Western Australia. The species compositions, species richness and catch rates of fishes in these estuaries, which vary markedly in their environmental characteristics, were analysed and compared to test the following hypotheses. 1) As the durations of mouth opening vary markedly among the five estuaries, the contributions of marine species to both the number of fish species and number of individuals in the five estuaries differ, thus leading to pronounced inter-estuarine differences in ichthyofaunal compositions. 2) The marked differences between the physico-chemical characteristics of the basins and rivers of each estuary, and a pronounced tendency for certain species to occupy one or the other of those regions, are reflected in conspicuous differences between the compositions of their fish faunas, irrespective of whether the estuary is permanently open, seasonally open or normally closed. 3) Interannual variations in ichthyofaunal composition occur either when the physico-chemical characteristics of an estuary change progressively with time and/or certain species move into offshore, deeper waters. 4) Seasonal changes in the compositions of the fish faunas are most pronounced in those estuaries that undergo the greatest changes in physico-chemical characteristics during the year. 5) As salinities vary less and stay higher in the basins than rivers, many marine species tend to remain in the basins and consequently species richness is greater in that region of the estuary than in the rivers. 6) Catch rates of fishes are relatively low in the most oligotrophic estuary and relatively high in estuaries with the greatest primary productivity.

2. Materials and methods

2.1. Sampling localities and regime

The fishes in offshore, deeper waters of the basins and main tributaries of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary on the south coast of Western Australia (Fig. 1) were sampled seasonally between summer 2006 and autumn 2007. The basin sites included one in the short but well defined entrance channels of both the Broke and Irwin inlets. The areas of the basins ranged from 2.5 km^2 in Wellstead Estuary to 10 and 16 km^2 in Irwin Inlet and Oyster Harbour, respectively, to 48 km^2 in the large Broke and Wilson inlets. The number of sites selected to provide representative samples of the fish faunas of offshore waters in the basins thus ranged from 5 in Wellstead Estuary to 8 and 10 in the Broke and Wilson inlets, respectively (Fig. 1). As the estuarine regions of the principal tributaries of the five estuaries are of similar length, three sites were selected for sampling that region in each estuary.

Fishes were sampled using sunken composite multifilament gill nets, comprising 20 m panels, each with a height of 2 m, but containing a different stretched mesh size, i.e. either 35, 51, 63, 76, 89 or 102 mm. Gill nets were set in the Broke, Irwin and Wilson inlets and Oyster Harbour at dusk and retrieved ca 12 h later around dawn. However, as preliminary sampling in 2005 demonstrated that gill nets set overnight would yield far greater and unacceptably high catches in Wellstead Estuary than in the other four estuaries, the gill nets in this estuary were set for only 1 h from dusk. Salinity, water temperature and dissolved oxygen concentration were measured at the surface and bottom of the water column at each sampling site on each sampling occasion using a Yellow Springs International Model 85 Oxygen, Conductivity, Salinity and Temperature Meter.

Fishes were euthanased in an ice slurry immediately after capture and transported to the laboratory where they were frozen until processing. Each fish was subsequently identified to species and its total length (TL) recorded to the nearest 1 mm. Each species was allocated to one of the following life-cycle guilds (categories) defined by Elliott et al. (2007) and using the life-cycle designations provided by Potter and Hyndes (1999) for the various species in south-western Australia or, in the case of the few species not included in that review, those derived from the results of recent studies. Marine stragglers (MS), i.e. species that spawn at sea and typically enter estuaries irregularly and only in low numbers; marine migrants (MM), i.e. species that spawn at sea and often enter estuaries in large numbers and particularly as juveniles; estuarine residents (ER), i.e. species typically found only in estuaries and which thus complete their life cycles within the estuarine environment; estuarine residents and marine species (ER&M), i.e. species represented by discrete populations in both estuarine and marine waters; freshwater stragglers (FS), i.e. freshwater species that are found in estuaries and usually only in low numbers and in their low salinity, upper reaches.

2.2. Multivariate analyses

The mean percentage contributions of each species to the catches of fishes obtained from both the basins and the rivers of

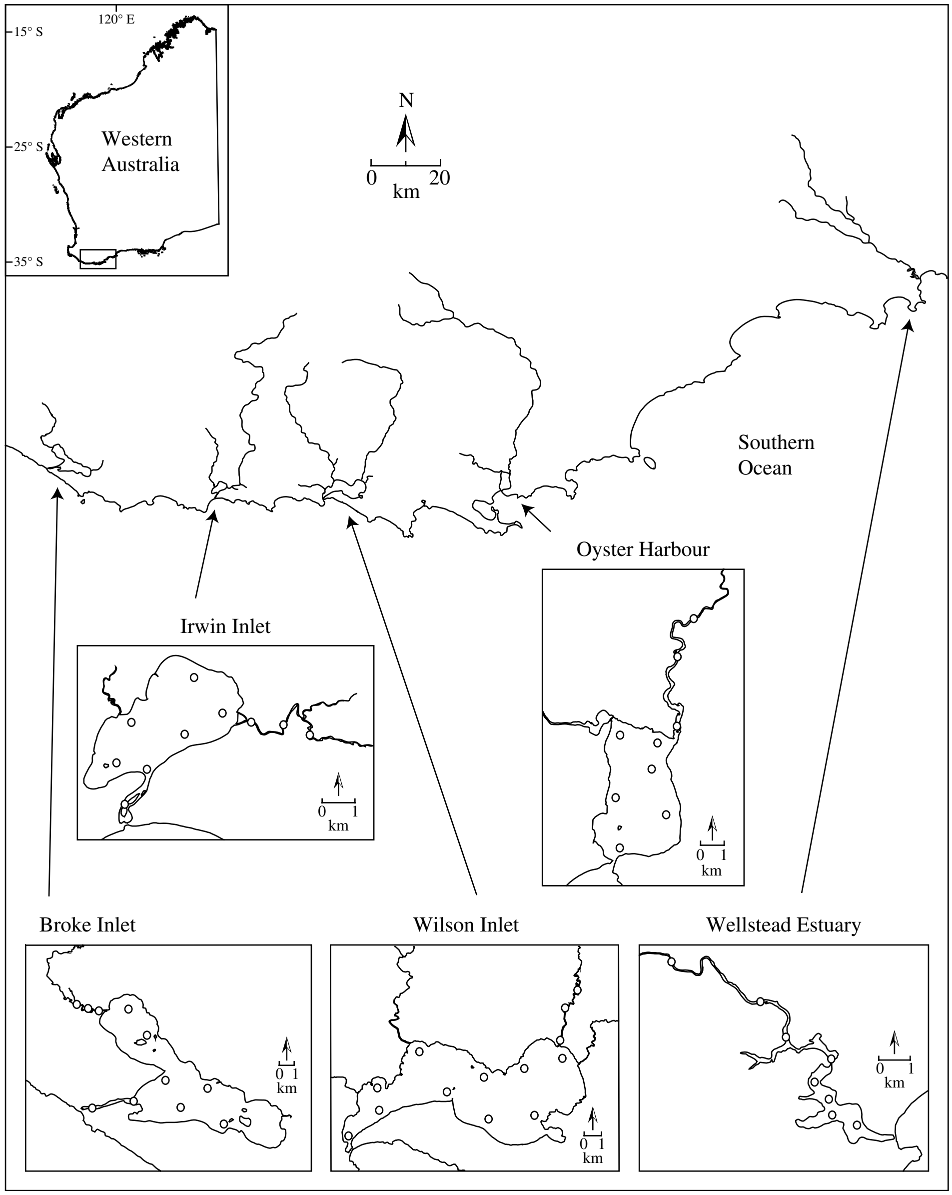

Fig. 1. Maps showing the location of Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary on the south coast of Western Australia and the location of sampling sites (circles) in those estuaries.

each of the five estuaries in each season of each year of sampling were square root transformed and employed to construct a Bray–Curtis resemblance matrix using PRIMER v6.1.2 (Clarke and Gorley, 2006). This transformation was shown to be appropriate from the relationship between the $\log_{10}$ of the standard deviation and the $\log_{10}$ of the mean percentage contribution of each species to the total catch in the basin and river of each estuary in each season of both years (see Clarke and Warwick, 2001). The above matrix was subjected to permutational analysis of variance (PERMANOVA) (Anderson et al., 2008) to facilitate a preliminary exploration as to whether there were significant interactions between estuary, region of estuary (basin vs river), year and/or season and, if so, the strength of those interactions compared with that of any significant main effects.

The above matrix was next subjected to non-metric multidimensional scaling (nMDS) ordination (Clarke, 1993; Clarke and Gorley, 2006) to explore visually the extent to which, overall, the species composition differed between region of estuary and between estuaries, which were shown by PERMANOVA to be by far the most important factors influencing ichthyofaunal composition (see Section 3.4). Two-way crossed analysis of similarity (ANOSIM) (Clarke, 1993), using a Bray–Curtis resemblance matrix derived from the percentage contribution of the various fish species to each replicate sample, was then used to determine the relative importance of each of the above four factors, without the confounding effects of the other three factors. This involved using, in turn, each factor vs a combination of the other three factors, which thereby removed their combined effects. Note that this type of approach was adopted for all subsequent two-way crossed ANOSIMs when more than two factors were involved and that, in order to obtain sufficient permutations for these ANOSIM tests, they used the percentage contributions of each species in each replicate sample, rather than the mean of those replicates. The influence on ichthyofaunal compositions of estuarine region, the most important of the above four factors (see Section 3.4), was then examined individually for each estuary using two-way crossed ANOSIM tests.

A matrix constructed from the mean percentage contributions of the various species to the fish faunas in the basins of the five estuaries was then subjected to nMDS ordination. Two-way crossed ANOSIMs were employed to determine whether the fish faunas of the basins differed significantly among estuaries, years and seasons. Pairwise ANOSIMs were then used to explore the extent of any differences between the ichthyofaunal compositions of the basins in each pair of estuaries. The above procedure was then adopted for the riverine ichthyofauna in the five estuaries.

Two-way crossed ANOSIMs and nMDS ordinations were used to further explore the influence of year and season on the compositions of the fish faunas within each region of each estuary separately. In all ANOSIM tests, particular emphasis was placed on the R statistic values determined by those tests. R statistic values close to 1 demonstrate that the composition of a priori groups of samples are very different, whereas those close to 0 show that such groups are very similar.

Similarity percentages (SIMPER) were used to determine the species that best typified the ichthyofaunas of a priori groups and those that best distinguished between the ichthyofaunal compositions of those groups (Clarke, 1993). Where appropriate, multivariate dispersion (MVDISP) was used to compare the extent of the variability in the compositions of the fish faunas in the basins and rivers of the five estuaries (Somerfield and Clarke, 1997).

Biota and environment matching (BIOENV) (Clarke and Warwick, 2001) was employed to elucidate which of certain environmental variables or combination of those variables provided the best correlation with the underlying pattern of distribution (rank order of similarity) of ichthyofaunal compositions in the various samples. These variables were salinity, water temperature and dissolved oxygen concentration at the surface and bottom of the water column, number of days that the mouth had been open prior to each sampling occasion and whether or not substantial macrophyte growths were present. For this procedure, Euclidean matrices, constructed from each combination of square root transformed and normalised data for the environmental variables, were matched against the Bray–Curtis similarity matrix constructed using the square root transformed percentage contributions of each fish species in each of the corresponding replicate samples.

2.3. Univariate analyses

The species richness (number of species) and catch rate of fishes in each replicate sample from the basin and river of the Broke, Irwin and Wilson inlets and Oyster Harbour in each season of 2006 and 2007 were both subjected to four-way analysis of variance (ANOVA). These ANOVAs thus determined whether the species richness and/or catch rates of fishes were influenced significantly by estuary, region of estuary (basin vs river), season and/or year, each of which was considered a fixed factor. Note that because gill nets had to be set for a far shorter period in Wellstead Estuary, i.e. 1 vs 12 h, and would thus have yielded values for particularly catch rates that would not have been directly comparable with those for the other four estuaries, the species richness and catch rates for Wellstead Estuary were subjected to separate three-way ANOVAs to elucidate whether estuary region, year and/or season influenced the species richness and/or catch rate of fishes in this system.

Prior to subjecting species richness and catch rates to ANOVA, the data for these variables were square root and fourth root transformed, respectively. These transformations were shown to be appropriate from the relationship between the $\log_{10}$ of the standard deviation and $\log_{10}$ of the mean for the values for each biotic variable in the replicate samples obtained seasonally from the basin and river of each estuary in each year (see Clarke and Warwick, 2001). When there were significant interactions ($p < 0.05$), Scheffé's multiple comparison tests were used to determine whether the differences in the means were significant.

3. Results

3.1. Environmental characteristics of the five estuaries

The periods during which the five estuaries were open to the ocean varied markedly during this study. Thus, Oyster Harbour was always open, whereas the Broke, Irwin and Wilson inlets were open for two or three periods and Wellstead Estuary was open only during the first two seasons (Fig. 2). Variations in the duration and size of mouth opening of the seasonally-open and normally-closed estuaries largely reflect differences in the volume of riverine discharge and, in the case of the Broke, Irwin and Wilson inlets, the water level at which the sand bar is artificially breached. These marked variations account for the salinity regimes differing markedly among those estuaries and particularly in the degree to which salinity varies during the year.

Mean salinities at the surface and bottom of the water column in the basins of each estuary were always the same or similar in any given season (Fig. 2). Mean seasonal salinities in the basins of the Broke and Irwin inlets ranged widely from minima of 8–10 to maxima of 38–40, whereas those of Wilson Inlet, Oyster Harbour and Wellstead Estuary ranged only from 15–25, 30–37 and 30–45, respectively (Fig. 2). In contrast to the situation in the basins, marked haloclines formed in the rivers of each estuary, except for that of Wellstead Estuary, with maximum differences between the surface and bottom of the water column in the Broke, Irwin and Wilson Inlets and Oyster Harbour typically occurring in winter and ranging from 14 to 26 (Fig. 2). The trends exhibited throughout the year by salinities at the bottom of the water column in the rivers paralleled those in their respective basins, but with salinities in any given season typically being lower in the rivers.

Mean seasonal water temperatures in the basins and rivers of each of the five estuaries underwent the same pattern of change in both years, declining from maxima of 23–25 °C in summer or autumn to minima of 11–13 °C in winter or spring. Thermoclines were present in autumn and winter in the rivers of each estuary except that of Wellstead Estuary.

In both years, the mean seasonal concentrations of dissolved oxygen underwent the same clearly defined pattern of change in the basins of each estuary, with values at the surface and bottom of the water column rising from their minima of 4–6 mg L^{-1} in summer to their maxima of 6–9 mg L^{-1} in winter. The concentrations of dissolved oxygen at the surface of the water column of the rivers were similar to those of the basins in the corresponding seasons. However, oxyclines formed in the river of each estuary during most seasons, with the maximum difference between the dissolved oxygen concentrations at the surface and bottom of the water column being as high as 5.3 and 4.6 mg L^{-1} in Irwin and Wilson inlets, respectively.

The characteristics of the five estuaries fulfil the following definition that was provided by Day (1980) for an estuary and which represented a modification of that given by Pritchard (1967) based on the features of northern hemisphere estuaries. "An estuary is a partially enclosed body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with freshwater derived from land drainage". This definition accommodates the marked differences between the morphological and physico-chemical characteristics of estuaries in temperate regions of southern Africa and southern Australia and those typically found in estuaries, particularly, of the temperate regions of the northern hemisphere.

The rank order of similarity of the ichthyofaunal compositions at the various sampling sites were shown by BIOENV to be better correlated with a combination of surface salinity, duration of sand bar opening prior to sampling and whether or not macrophytes

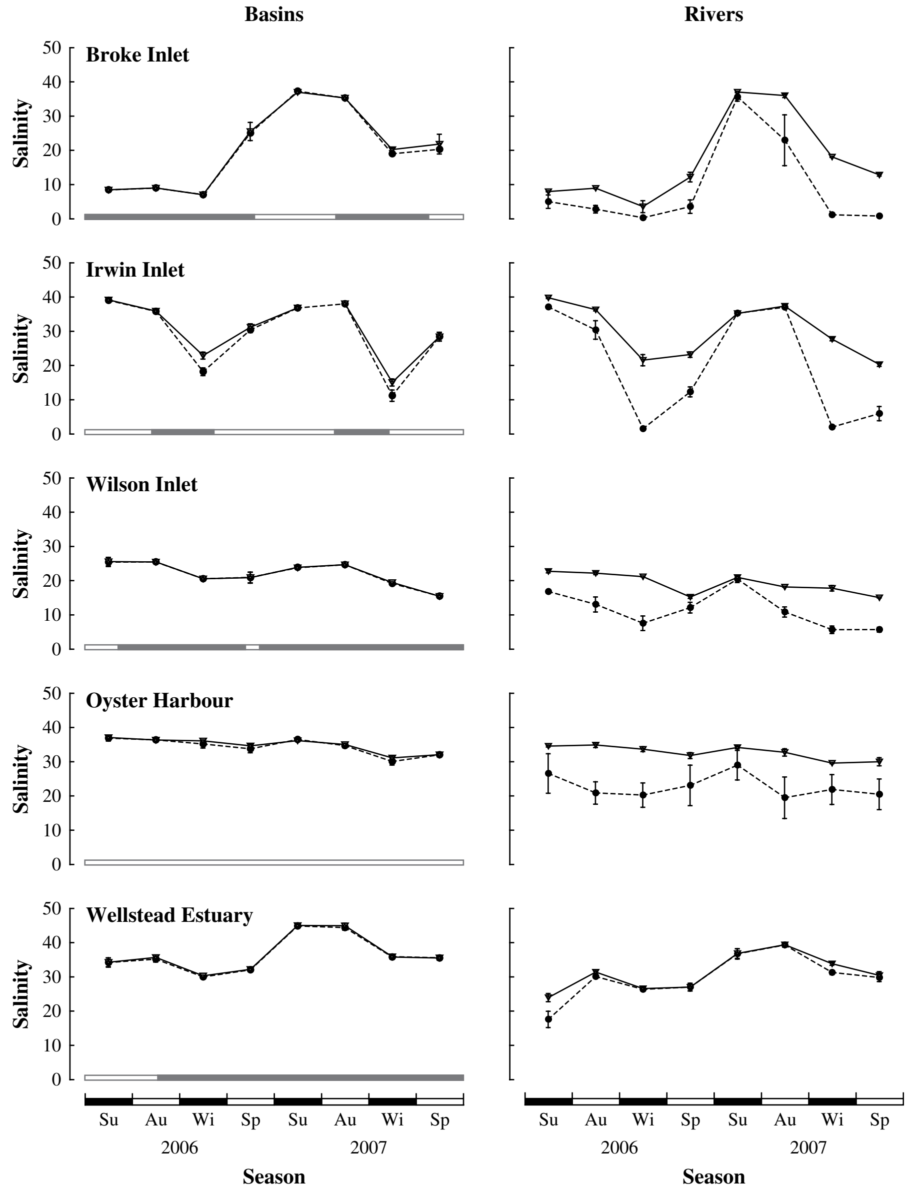

Fig. 2. Mean seasonal salinities ± 1SE at the surface (dashed line) and bottom (solid line) of the water column in the basins and rivers of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. Open and closed bars on the *x*-axis of the basin plots for each estuary denote when the mouth of that estuary was open and closed, respectively.

were abundant ($p = 0.010$, $\rho = 0.315$) than with any individual variable or other combination of variables. Although these results demonstrate that the above three variables influence ichthyofaunal composition in south coast estuaries, the ρ value was not high, which implies either that other important, but less tangible factors were contributing to the variations in composition and/or that certain fish species behave differently in different types of estuaries.

3.2. Contributions of the various species to the fish faunas of the five estuaries

A total of 22,329 individuals and 58 species of fish were caught by seasonal gill netting over two years in the basins and rivers of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary (Table 1). The majority of these fishes were collected from the basin region of each estuary, with a total of 15,717 individuals and 57 species of fish being caught in this region (Table 1). The total number of fishes caught in the basin of each estuary ranged from 1638 in Broke Inlet to 4324 in Irwin Inlet, while the total number of fish species ranged from 17 in Wellstead Estuary to 45 in Oyster Harbour (Table 1). Note however, that because of marked differences in the sizes of these estuaries, the number of sites selected to obtain representative samples for each estuary differed (Fig. 1) and that this would have influenced the numbers of fishes and, to a lesser extent, also the numbers of fish species caught.

Within the basins, the most abundant species in the Broke, Irwin and Wilson inlets and Wellstead Estuary was *Aldrichetta forsteri*, whereas *Pelates sexlineatus* was the most abundant in Oyster Harbour (Table 1). Although the contributions of *A. forsteri* to the total catches in the basins of Broke Inlet and Wellstead Estuary were particularly high, it contributed only 1.7% to the catch in the basin of Oyster Harbour. *Arripis georgianus* contributed more than 9% to the catches in the basins of all but the Wellstead Estuary, and the same was true for *Mugil cephalus* and *Cnidoglanis macrocephalus* in two estuaries, and *Engraulis australis* in one estuary. *Acanthopagrus butcheri* made a far greater contribution to the fish fauna of the basin of Wellstead Estuary (25.4%) than to that of the

Table 1
Life-cycle guilds (L.G.) and percentage contributions of each fish species to the total catch from offshore, deeper waters of the basin and river of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. Numbers of sampling sites are given in parenthesis for each region of each estuary. MS = marine straggler, MM = marine migrant, ER&M = estuarine resident & marine, ER = estuarine resident, FS = freshwater straggler.

Species	L.G.	Basins					Rivers				
		Broke Inlet (8)	Irwin Inlet (7)	Wilson Inlet (10)	Oyster Harbour (6)	Wellstead Estuary (5)	Broke Inlet (3)	Irwin Inlet (3)	Wilson Inlet (3)	Oyster Harbour (3)	Wellstead Estuary (3)
Aldrichetta forsteri	MM	46.9	21.0	21.4	1.7	43.7		5.4	12.4	1.6	14.9
Mugil cephalus	MM	8.5	11.6	9.7	2.3	16.7	96.2	70.3	37.3	13.6	28.2
Acanthopagrus butcheri	ER		0.4	3.4	7.1	25.4	0.9	10.0	45.2	46.2	53.0
Arripis georgianus	MM	18.0	18.4	9.1	10.5	1.8	1.4	0.5	<0.1	0.6	
Cnidoglanis macrocephalus	ER&M		16.2	11.9	4.7	0.9		1.4	1.9		
Pelates sexlineatus	MM		5.6	8.2	28.8					1.1	
Engraulis australis	ER&M	2.9	1.0	15.8	0.3	0.3		0.3	0.8	3.5	2.2
Arripis truttaceus	MM	0.9	5.9	0.2	3.8	6.1		10.5	0.8	1.1	1.1
Pseudocaranx dentex	MM	6.8	7.4	0.2	8.3	0.1		0.6		0.1	
Platycephalus speculator	ER&M	0.1	0.3	7.7	1.1	0.1			0.1	0.1	
Ammotretis rostratus	ER&M	2.4	5.2	0.6	0.5	0.3		0.1	1.1	0.4	0.1
Sillaginodes punctata	MM	0.7	0.8	3.8	5.4	0.5					
Rhabdosargus sarba	MM	2.0	2.4	1.6	0.2	1.9		0.5	0.3	1.2	0.5
Argyrosomus japonicus	MM				1.1					27.8	
Trachurus novaezelandiae	MM				10.0					2.2	
Hyporhamphus melanochir	ER&M	5.3	0.7	2.8	0.1	<0.1					
Pagrus auratus	MM	0.6	0.8	1.6	0.1	0.1				0.2	
Gymnapistes marmoratus	MM	0.2			1.5	2.0				0.1	0.1
Platycephalus laevigatus	MM			<0.1	2.6						
Trygonoptera mucosa	MM				2.4						
Gonorynchus greyi	MM	0.2	0.2	0.7	0.3						
Pomatomus saltatrix	MM	0.1	0.6	0.4			0.5				
Acanthaluteres brownii	MS	0.1	0.1	0.2	1.1						
Meuschenia freycineti	MS	0.1	0.2	0.1	0.9	<0.1					
Pseudorhombus jenynsii	MM	0.9	0.2	0.1	0.2		0.5			0.1	
Sillago schomburgkii	MM	0.2	0.4	0.2	<0.1			0.3			
Haletta semifasciata	MS				1.1						
Heterodontus portusjacksoni	MS				0.8						
Aplodactylus westralis	MS	0.7	0.1								
Leviprora inops	MS				0.7						
Enoplosus armatus	MS	0.1	0.2	0.1	0.1						
Sphyraena novaehollandiae	MS				0.7						
Sillago bassensis	MS	0.9									
Chelidonichthys kumu	MS	0.6									
Trygonorrhina fasciata	MS				0.3						
Elops machnata	MM	0.1	0.1	<0.1	0.1						
Dactylophora nigricans	MS				0.3						
Nelusetta ayraudi	MS	0.3									
Aptychotrema vincentiana	MS				0.2						
Schuettea woodwardi	MS	0.2									
Cristiceps aurantiacus	MS		0.1								
Notolabrus parilus	MS			<0.1	<0.1						
Neosebastes pandus	MS				0.1						
Maxillicosta scabriceps	MS				0.1						
Achoerodus gouldii	MS		<0.1	<0.1	<0.1						
Contusus brevicaudus	MS		<0.1		<0.1						
Sphyrna zygaena	MS				<0.1						
Dasyatis brevicaudata	MS				<0.1						
Myliobatis australis	MS	0.1									
Perca fluviatilis	MS						0.5				
Upeneichthys vlamingii	MS				<0.1						
Kyphosus sydneyanus	MS	0.1									
Cheilodactylus vestitus	MS				<0.1						
Cheilodactylus rubrolabiatus	MS				<0.1						
Arenigobius bifrenatus	ER&M					<0.1					
Ammotretis elongatus	MS	0.1									
Acanthaluteres vittiger	MS				<0.1						
Marilyna pleurosticta	MS			<0.1							
Total number		1638	4324	3917	2351	3487	213	1527	2158	979	1735

Irwin and Wilson inlets and Oyster Harbour and was not caught in the basin of Broke Inlet (Table 1).

Concomitant sampling at three sites in each of the river regions of the five estuaries yielded a total of 6612 individuals and 20 species of fish. The total numbers of fishes obtained from this region of each estuary varied markedly from 213 in Broke Inlet to 979 in Oyster Harbour to between 1527 and 2158 in Irwin Inlet, Wellstead Estuary and Wilson Inlet (Table 1). The number of species recorded in the rivers ranged from 6 in Broke Inlet to 16 in Oyster Harbour. *Mugil cephalus* dominated the riverine catches in the Broke and Irwin inlets and was the second most abundant species in Wilson Inlet and Wellstead Estuary and the third most numerous in Oyster Harbour. However the contributions of this mugilid to the total catch ranged widely from 96.2% in Broke Inlet to 70.3% in Irwin

Inlet to 37.3 and 28.2% in Wilson Inlet and Wellstead Estuary, respectively, to only 13.6% in Oyster Harbour. *Acanthopagrus butcheri* replaced *M. cephalus* as the most abundant species in the river regions of Wilson Inlet, Oyster Harbour and Wellstead Estuary. Although *Argyrosomus japonicus* constituted more than 25% of the numbers caught in the tributary of Oyster Harbour, it was found neither in the rivers nor basins of the other four estuaries (Table 1). The two most abundant species in each river collectively contributed between 60 and 97% to the total catches in that region of their respective estuaries.

As in most studies of estuarine fish communities, the individual species have been ranked according to their contribution to the total numbers of fishes caught. While the ranking of most species remained similar in each system when using biomass, this did not apply to *Engraulis australis*, which was the smallest fish species caught by gill net and was invariably bridled rather than meshed. Thus, whereas this species ranked second in Wilson Inlet by numbers, it was only nineteenth in terms of biomass. Those differences reflect variations in percentage contributions of 15.8 vs 0.2%, respectively.

3.3. Contributions of different life-cycle guilds to the fish faunas of the five estuaries

The number of marine species varied markedly among the basins of the five estuaries (Table 2), reflecting, in part, differences in the type of estuary. Thus, in that region, the marine straggler and marine migrant categories were represented by only 1 and 9 species, respectively, in the normally-closed Wellstead Estuary, compared with as many as 21 and 18 species, respectively, in the permanently-open Oyster Harbour. However, in terms of species richness, marine species still dominated the fish faunas of the basin region of all five estuaries, with their collective contributions ranging from 58.8% in Wellstead Estuary to 86.7% in Oyster Harbour (Table 2). In contrast, the numbers of estuarine-spawning species in total (ER and ER&M) ranged only from 4 to 7, with the collective contribution of those two guilds being far greater in the basin of Wellstead Estuary (41.2%) than in that of any other estuary.

While no marine stragglers were caught in the river of any estuary, marine migrants were caught in this region of all five estuaries, with the number of such species ranging from 4 to 7 in the Broke, Irwin and Wilson inlets and Wellstead Estuary to 12 in Oyster Harbour and contributing between ca 50 and 75% to the total number of species in that region of all estuaries (Table 2). The total number of estuarine-spawning species collectively in the rivers ranged from 1 to 5 and contributed between 16.7% (Broke Inlet) and 50.0% (Wilson Inlet).

In terms of number of individuals, the ichthyofaunas in the basins of each estuary were dominated by marine species (and particularly marine migrants), with their contributions approaching 60% in Wilson Inlet and lying between 73 and 89% in each of the other four estuaries (Table 2). The contribution by estuarine-spawning species to the total numbers of fishes in the basins ranged widely from only 10.7% in Broke Inlet to 42.2% in Wilson Inlet. In the rivers, marine migrants contributed far more to the fish faunas of Broke Inlet (99%) and Irwin Inlet (88%) than to those of Wilson Inlet, Oyster Harbour and Wellstead Estuary, i.e. between 45 and 51% (Table 2). Conversely, estuarine-spawning species made far lower contributions in the rivers of the first two estuaries (<12%) than the latter three estuaries (45–53%).

3.4. Comparisons between the ichthyofaunal compositions in the basins and rivers

A preliminary analysis using PERMANOVA demonstrated that ichthyofaunal composition was influenced significantly by estuary, region of estuary and season, but not by year and that there were significant two-way interactions between estuary and each of region of estuary, year and season and between region of estuary and season (Table 3). The mean squares were far higher for region of estuary than estuary, which in turn, were higher than the

Table 2
Contributions of the number of species and number of individuals of the different life-cycle guilds to the ichthyofaunal compositions of the offshore, deeper waters of the basins and rivers of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. MS = marine straggler, MM = marine migrant, ER&M = estuarine resident & marine, ER = estuarine resident, FS = freshwater straggler.

		Basins					Rivers				
		Broke Inlet	Irwin Inlet	Wilson Inlet	Oyster Harbour	Wellstead Estuary	Broke Inlet	Irwin Inlet	Wilson Inlet	Oyster Harbour	Wellstead Estuary
Number of species											
MS	Number	11	7	6	21	1					
	Contribution (%)	37.9	25.9	22.2	46.7	5.9					
MM	Number	14	14	15	18	9	4	7	5	12	5
	Contribution (%)	48.3	51.9	55.6	40.0	52.9	66.7	63.6	50.0	75.0	62.5
ER&M	Number	4	5	5	5	6		3	4	3	2
	Contribution (%)	13.8	18.5	18.5	11.1	35.3		27.3	40.0	18.8	25.0
ER	Number		1	1	1	1	1	1	1	1	1
	Contribution (%)		3.7	3.7	2.2	5.9	16.7	9.1	10.0	6.3	12.5
FS	Number						1				
Contribution (%)							16.7				
Total number of species		29	27	27	45	17	6	11	10	16	8
Number of individuals											
MS	Number	53	34	19	159	1					
	Contribution (%)	3.2	0.8	0.5	6.8	<0.1					
MM	Number	1410	3255	2243	1865	2545	210	1347	1098	488	776
	Contribution (%)	86.1	75.3	57.3	79.3	73.0	98.6	88.2	50.9	49.8	44.7
ER&M	Number	175	1018	1521	159	57		28	85	39	40
	Contribution (%)	10.7	23.5	38.8	6.8	1.6		1.8	3.9	4.0	2.3
ER	Number		17	134	168	88	2	152	975	452	919
	Contribution (%)	0.4	3.4	7.1	25.4	0.9	10.0	45.2	46.2	53.0	
FS	Number						1				
	Contribution (%)						0.5				
Total number of individuals		1638	4324	3917	2351	3487	213	1527	2158	979	1735

Table 3
Mean squares and significance levels for four-way PERMANOVA of the ichthyofaunal compositions at sites in the basin and river regions of offshore, deeper waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary in each season of 2006 and 2007. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

	Main effects					
	Estuary (E)	Region (R)	Year (Y)	Season (S)		Residual
df	4	1	1	3		12
Composition	11,468.0***	46,301.0***	908.2	1090.1*		458.8
	Two-way interactions					
	E × R	E × Y	E × S	R × Y	R × S	Y × S
df	4	4	12	1	3	3
Composition	5240.6***	816.6*	871.1*	462.9	857.5*	697.5
	Three-way interactions					
	E × R × Y	E × R × S		E × Y × S	R × Y × S	
df	4	12		12	3	
Composition	589.9	539.4		406.0	422.3	

interaction between estuary and region of estuary, which was the only interaction that was moderately strong. Year was not significant and the influence of season was relatively small (Table 3).

After the matrix, derived from the mean contributions of the various species to each seasonal sample from the basin and river of each estuary, had been subjected to ordination, the samples from each of the basins lay in the lower part of the plot and showed essentially no overlap with those of the rivers, which occupied the upper part of the plot (Fig. 3a). When the same data were coded for estuary, the samples from the Broke, Irwin and Wilson inlets and Oyster Harbour formed vertical and essentially discrete groups that progressed from left to right on the ordination plot (Fig. 3b). Although the samples from Wilson Inlet and Wellstead Estuary intermingled in the top part of the plot, those for these two estuaries in the lower part of the plot, which corresponded to samples from their basins, formed discrete groups (cf Fig. 3a, b), which helps to explain the basis for the estuary × region interaction. The samples for neither year nor season tended to form distinct groups on the ordination plot when the data were coded separately for these two variables (plots not shown).

Two-way crossed ANOSIM tests using each factor in turn vs a combination of the other three factors yielded Global R statistic values of 0.574 for region of estuary ($p = 0.001$), 0.507 for estuary ($p = 0.001$), 0.180 for season ($p = 0.001$) and 0.122 for year ($p = 0.001$). Comparisons of the results for two-way crossed ANOSIM tests for region vs year and season combined in each estuary demonstrated that the extents of the differences in the compositions of the fish faunas in the basin and river varied among estuaries. Thus, this regional difference was greatest in Irwin Inlet (0.808), followed by Oyster Harbour (0.633), Broke Inlet (0.598) and Wellstead Estuary (0.528) and was least in Wilson Inlet (0.441).

The presence of relatively greater contributions and frequencies of occurrence of *Mugil cephalus* distinguished the faunas of the river from the basin in each estuary except Oyster Harbour and the same was true for *Acanthopagrus butcheri* in all but Broke Inlet. In contrast, *Arripis georgianus* was caught in consistently greater numbers in the basins than rivers in each of the five estuaries and this was also the case for *Cnidoglanis macrocephalus* in Irwin Inlet, Wilson Inlet and Oyster Harbour and for *Aldrichetta forsteri* in the Broke and Irwin inlets and Wellstead Estuary and for *Pelates sexlineatus* in Wilson Inlet and Oyster Harbour. Consistently greater numbers of *Argyrosomus japonicus* distinguished the river from the basin of Oyster Harbour, while the reverse trend was exhibited by *Engraulis australis* in Wilson Inlet, *Arripis truttaceus* in Wellstead Estuary and *Pseudocaranx dentex* and *Sillaginodes punctata* in Oyster Harbour.

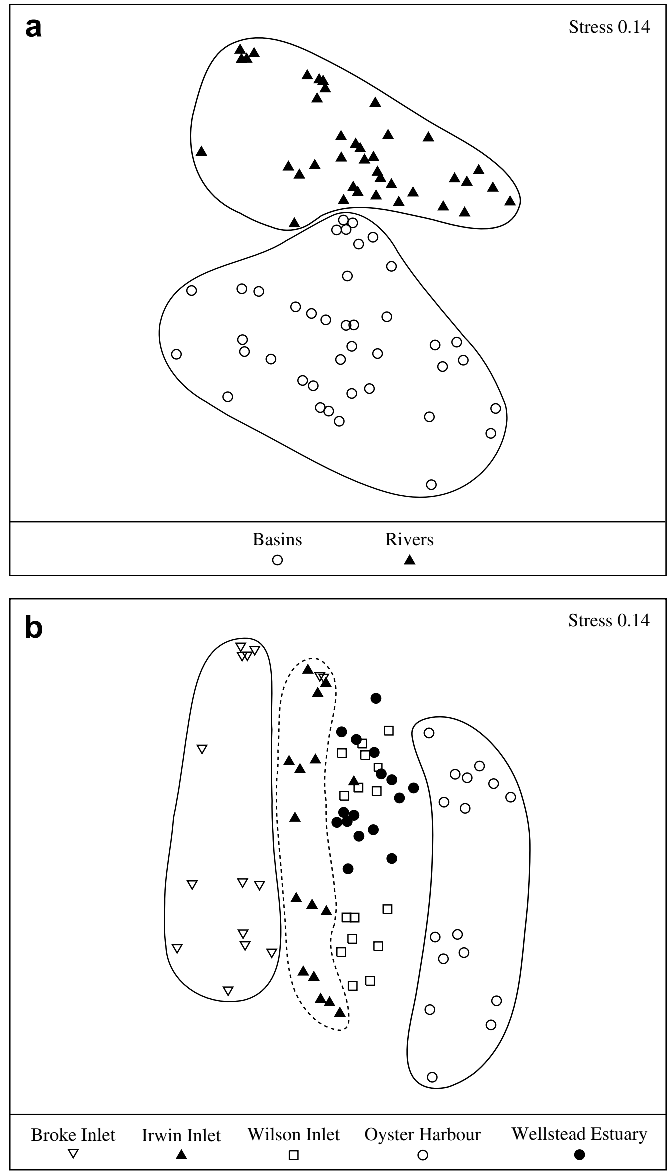

Fig. 3. Non-metric multidimensional scaling ordination plots constructed from the matrix derived from the mean percentage contributions of each species to the catches obtained in each season of each year from offshore, deeper waters of Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. Samples are coded for a) rivers and basins and b) each estuary. NB. In both a) and b) an extreme outlying sample from the river of Broke Inlet has been excluded from the ordination.

3.5. *Comparisons of the ichthyofaunal compositions in the basins of the five estuaries*

After the matrix, constructed from the mean contributions of the various fish species to the basin samples from the five estuaries, had been subjected to ordination, the samples for each estuary formed discrete groups on the ordination plot (Fig. 4a). Furthermore, the samples from Broke, Irwin and Wilson inlets and Oyster Harbour formed groups that progressed from left to right on the ordination plot, i.e. according to their west to east location on the south coast of Western Australia (Fig. 1). In contrast, the samples from Wellstead Estuary, the most easterly and geographically discrete of the five estuaries, lay in the top quarter of the plot immediately above those from Wilson Inlet and above all samples from each of the other estuaries, except for two of those from Broke Inlet. The samples from Broke Inlet were the most widely

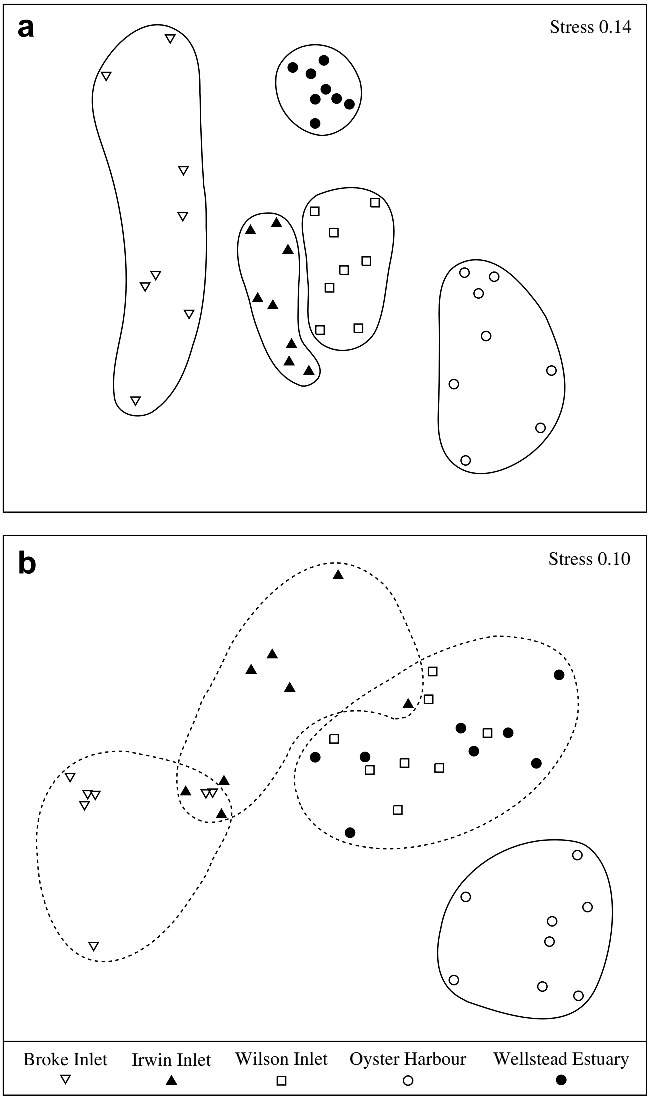

Fig. 4. Non-metric multidimensional scaling ordination plots of the matrices derived from the mean percentage contribution of each species to each replicate sample obtained in each season of each year from offshore, deeper waters of a) the basins and b) the rivers of Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary.

dispersed, while those from Wellstead Estuary were the least dispersed (Fig. 4a), which is reflected in their respective MVDISP values of 1.67 and 0.35.

A two-way crossed ANOSIM test, involving data for estuary vs year and season combined, produced a Global R statistic of 0.507 and thus confirmed that the ichthyofaunal compositions of the basins of the five estuaries were significantly different ($p = 0.001$). Furthermore, pairwise ANOSIM comparisons demonstrated that the ichthyofaunal compositions of the basins of each pair of estuaries were significantly different, i.e. all $p = 0.001$, with the R statistic values ranging from 0.358 for Irwin Inlet vs Wilson Inlet to 0.746 for Irwin Inlet vs Wellstead Estuary (Table 4).

Although *Aldrichetta forsteri* was among the two most important typifying species in the basins of all five estuaries except Oyster Harbour, *Arripis georgianus* and *Cnidoglanis macrocephalus* were the only other species to rank highly as typifying species in the basin of more than one estuary (Table 4). The fourth and fifth most important typifying species in the basins include several, which, like *A. forsteri*, *A. georgianus* and *Cnidoglanis macrocephalus*, are fished commercially in south coast estuaries, i.e. *Mugil cephalus* in Broke Inlet, *Ammotretis rostratus* in Irwin Inlet, *Platycephalus speculator* and *A. georgianus* in Wilson Inlet and *C. macrocephalus* and *Sillaginodes punctata* in Oyster Harbour.

Engraulis australis and *Platycephalus speculator* were consistently abundant only in catches obtained from the basin of Wilson Inlet, and thus distinguished the ichthyofaunal composition of this basin from that of each of the other four estuaries (Table 4). Similarly, the consistently high contributions of *Pseudocaranx dentex* and *Cnidoglanis macrocephalus* in Irwin Inlet and of *Pelates sexlineatus* and *Trachurus novaezelandiae* in Oyster Harbour distinguished the ichthyofaunal compositions of the basins of these estuaries from those of each other estuary. The consistently high contribution of a single species, *Acanthopagrus butcheri*, distinguished the fauna of the basin of Wellstead Estuary from that of each of the other estuaries. While consistently higher contributions of *Aldrichetta forsteri* distinguished the ichthyofauna of the basin of Broke Inlet from those of Irwin Inlet, Wilson Inlet and Oyster Harbour, a relatively lower contribution of this species distinguished the fish fauna of the basin of Broke Inlet from that of Wellstead Estuary (Table 4).

3.6. Comparisons of the ichthyofaunal compositions in the rivers of the five estuaries

On the ordination plot, derived using the matrix constructed from the mean percentage contributions of the various species to the fish faunas of the river component of the five estuaries, the distributions of the samples progressed from left to right in an arc from Broke Inlet on the left to Irwin Inlet to a combination of Wilson Inlet and Wellstead Estuary and finally to Oyster Harbour on the extreme bottom right (Fig. 4b). Thus, as with the basins, they progressed from left to right in an eastwards direction according to their geographical location in each case apart from Wellstead Estuary. Although the samples from the river of Oyster Harbour formed a discrete group and those of Broke Inlet did not overlap those from Wilson Inlet and Wellstead Estuary, the samples from the latter two estuaries intermingled and there was some overlap between those from Irwin Inlet and Broke Inlet and, to a very limited extent, also Wilson Inlet.

A two-way crossed ANOSIM test, involving data for estuary vs year and season combined, demonstrated that the ichthyofaunal compositions of the rivers of the five estuaries were significantly different ($p = 0.001$), with a Global R statistic of 0.511. Pairwise ANOSIM tests showed that the differences between the ichthyofaunal compositions in the rivers of each pair of estuaries were significant, i.e. all $p < 0.01$ or 0.001. While the R statistic values for seven of the 10 pairwise tests between the riverine regions of the various estuaries were ≥ 0.500, they were lower for Broke Inlet vs Irwin Inlet (0.443), Wilson Inlet vs Irwin Inlet (0.407) and only 0.255 for Wilson Inlet vs Wellstead Estuary (Table 5).

Mugil cephalus was one of the three most important typifying species in the river of each estuary and the same was true for *Acanthopagrus butcheri* in each estuary except Broke Inlet (Table 5). The only other species to rank among the two most important typifying species in the rivers of the various estuaries was *Argyrosomus japonicus* in Oyster Harbour, the only estuary in which this sciaenid was caught (Table 1).

Relatively low contributions and a very low frequency of occurrence of *Acanthopagrus butcheri* distinguished the ichthyofaunal composition in the river of Broke Inlet from that of all other estuaries, while consistently greater numbers of this sparid distinguished the composition of the river of Wellstead Estuary from that of each other estuary except Oyster Harbour (Table 5). *Argyrosomus japonicus* distinguished the ichthyofauna of the river of Oyster Harbour from the river of each of the other estuaries. Although the consistently greater contribution of *Aldrichetta forsteri*

Table 4
R Statistic values and significance levels for pairwise ANOSIMs for the ichthyofaunal compositions of the basins of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary derived from the matrix constructed using the percentage contributions of the various fish species to each replicate sample. The species determined by SIMPER as most responsible for typifying the ichthyofaunal compositions of the basins of individual estuaries (non-shaded boxes) and for distinguishing between the ichthyofaunal compositions in each pairing of those five estuaries (shaded boxes). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Estuary	Broke Inlet	Irwin Inlet	Wilson Inlet	Oyster Harbour	Wellstead Estuary
Broke Inlet	*A. forsteri* *A. georgianus* *M. cephalus*				
Irwin Inlet	0.495*** *C. macrocephalus* *A. forsteri*[a] *P. dentex* *P. sexlineatus* *A. truttaceus*	*A. georgianus* *A. forsteri* *C. macrocephalus* *A. rostratus*			
Wilson Inlet	0.479*** *C. macrocephalus* *A. forsteri*[a] *E. australis* *P. sexlineatus* *P. speculator*	0.358*** *E. australis* *P. speculator* *P. dentex*[a] *A. truttaceus*[a] *C. macrocephalus*[a] *M. cephalus*	*A. forsteri* *E. australis* *C. macrocephalus* *P. speculator* *A. georgianus*		
Oyster Harbour	0.739*** *P. sexlineatus* *A. forsteri*[a] *T. novaezelandiae* *A. butcheri* *A. georgianus*[a] *C. macrocephalus* *P. dentex*	0.626*** *A. forsteri*[a] *P. sexlineatus* *T. novaezelandiae* *A. butcheri* *P. dentex*[a] *M. cephalus*[a] *C. macrocephalus*[a]	0.508*** *A. forsteri*[a] *E. australis*[a] *T. novaezelandiae* *P. sexlineatus* *P. dentex* *P. speculator*[a] *M. cephalus*[a]	*P. sexlineatus* *A. georgianus* *T. novaezelandiae* *C. macrocephalus* *S. punctata*	
Wellstead Estuary	0.493*** *A. butcheri* *A. georgianus*[a] *A. forsteri* *A. truttaceus*	0.746*** *A. butcheri* *C. macrocephalus*[a] *A. georgianus*[a] *P. dentex*[a]	0.468*** *E. australis*[a] *A. butcheri* *P. sexlineatus*[a] *P. speculator*[a] *C. macrocephalus*[a]	0.732*** *A. forsteri* *P. sexlineatus*[a] *A. butcheri* *T. novaezelandiae*[a] *M. cephalus*	*A. forsteri* *A. butcheri*

[a] Denotes that the species makes a greater contribution to the ichthyofaunal composition of the estuary at the top of the column.

distinguished the ichthyofauna of the river of Wellstead Estuary from that of each of the other estuaries, frequently greater abundances of the mugilid *Mugil cephalus* distinguished the fish faunas of Broke, Irwin and Wilson inlets from that of Wellstead Estuary but not from that of Oyster Harbour (Table 5).

3.7. Interannual and seasonal comparisons of ichthyofaunal compositions

Two-way crossed ANOSIMs, using the matrix constructed from data for replicate samples, demonstrated that the ichthyofaunal compositions of the basin of each estuary differed significantly between years and among seasons, except in the case of year in Wilson Inlet and Oyster Harbour (Table 6). However, the R statistic values only exceeded 0.2 in the case of season in Broke Inlet, year in Wellstead Estuary and year and season in Irwin Inlet (Table 6). On the ordination plots derived from the data for Irwin Inlet, the samples for 2007 tended to lie in the middle of those for 2006 (Fig. 5a). In 2006, most of the samples for each season in the basin of Irwin Inlet formed groups that progressed sequentially in an anticlockwise direction according to season (Fig. 5b). In 2007, the samples for summer, winter and spring also formed groups that pursued an anticlockwise track on the ordination plot, while those for autumn were widely dispersed but tended to be closer to those of spring and summer rather than winter (Fig. 5c).

In the case of the rivers, two-way crossed ANOSIMs, employing year and season as factors, showed that ichthyofaunal composition was significantly influenced by year and season in Wellstead Estuary and by season in Irwin Inlet. The Global R statistic values for year (0.528) and season (0.398) in Wellstead Estuary were far greater than for season (0.259) in Irwin Inlet (Table 6). On the ordination plot for the river of Wellstead Estuary, 8 of the 12 samples for 2006 lay to the left of all of the 12 samples for 2007 (Fig. 6a), while the samples for the four seasons in that river tended to progress sequentially in both years (Fig. 6b, c).

3.8. Species richness and catch rates of fishes

Four-way ANOVA demonstrated that species richness differed significantly between Broke, Irwin and Wilson inlets and Oyster Harbour and also between region (basin vs river) and seasons but not years (Table 7). The mean square was far greater for region than estuary, which in turn was far greater than that for both season and the interaction between estuary and region. There was a small but significant three-way interaction between estuary, region and season (Table 7).

In each of the above four estuaries, the mean value for species richness was greater in the basin than river in each season (Fig. 7). These regional differences were significant in all four seasons in Broke Inlet, two of the seasons in both Irwin Inlet and Oyster Harbour and in none of the seasons in Wilson Inlet. The three-way interaction between estuary, region and season was no longer significant when Irwin Inlet was removed from the analyses, demonstrating that the very marked decline in the mean species richness in Irwin Inlet in winter (Fig. 7) was largely responsible for this interaction and indeed the overall seasonal effect.

The mean species richness in both the basin and river of Broke Inlet in each season were less than those in the corresponding regions of Irwin and Wilson inlets and Oyster Harbour and, in most seasons, these differences were significant. Furthermore, in each

Table 5
R statistic values and significance levels for pairwise ANOSIMs for the ichthyofaunal compositions of the rivers of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary derived from the matrix constructed using the percentage contributions of the various fish species to each replicate sample. The species determined by SIMPER as most responsible for typifying the ichthyofaunal compositions of the rivers of individual estuaries (non-shaded boxes) and for distinguishing between the ichthyofaunal compositions in each pairing of those five estuaries (shaded boxes). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Estuary	Broke Inlet	Irwin Inlet	Wilson Inlet	Oyster Harbour	Wellstead Estuary
Broke Inlet	*M. cephalus*				
Irwin Inlet	0.443*** *A. butcheri* *A. truttaceus* *A. forsteri* *C. macrocephalus*	*M. cephalus* *A. butcheri*			
Wilson Inlet	0.630*** *A. butcheri* *M. cephalus*[a] *A. forsteri*	0.407*** *A. butcheri* *M. cephalus*[a] *A. forsteri* *A. truttaceus*[a] *C. macrocephalus*	*A. butcheri* *M. cephalus* *A. forsteri*		
Oyster Harbour	0.773*** *A. butcheri* *M. cephalus*[a] *A. japonicus*	0.694*** *A. japonicus* *M. cephalus*[a] *A. butcheri* *A. truttaceus* *A. forsteri*[a]	0.500*** *A. japonicus* *M. cephalus*[a] *A. forsteri*[a] *C. macrocephalus*[a] *T. novaezelandiae*	*A. butcheri* *A. japonicus* *M. cephalus* *E. australis*	
Wellstead Estuary	0.736*** *A. butcheri* *M. cephalus*[a]	0.625** *A. butcheri* *M. cephalus*[a] *A. forsteri*	0.255** *A. forsteri* *M. cephalus*[a] *C. macrocephalus*[a] *A. butcheri*	0.597*** *A. japonicus*[a] *A. forsteri* *M. cephalus* *E. australis*[a]	*A. butcheri* *M. cephalus* *A. forsteri*

[a] Denotes that the species makes a greater contribution to the ichthyofaunal composition of the estuary at the top of the column.

season, the mean species richness in the basins of Irwin Inlet and Oyster Harbour were greater than those in this region in Wilson Inlet (Fig. 7) and these differences were usually significant.

Four-way ANOVA demonstrated that the catch rates of fishes differed significantly between estuaries, regions, years and seasons (Table 7). The mean square was far greater for estuary than the estuary × region interaction, which in turn was greater than those for both region and season. The mean squares for both of the other significant two-way interactions and the significant three-way interactions were relatively low (Table 7).

The catch rates in both the basin and river of Broke Inlet were less than those in the corresponding regions of each of the other three estuaries and these differences were frequently significant (Fig. 8). The catch rates in the basin of Irwin Inlet were greater than those in Oyster Harbour in all seasons and than those in Wilson Inlet in each season except summer and the catch rates in the rivers were greater in Wilson Inlet than in Oyster Harbour in all seasons and than in Irwin Inlet in all seasons except autumn (Fig. 8).

On the interaction plot for estuary × region × season, there was no consistent overall trend for catch rate to be greater in the basin than the river or vice versa. Thus, while the mean catch rate was greater in the basin than river in all seasons in Broke Inlet, the reverse was true for three seasons in Wilson Inlet and the catch rates were very similar in the river and basin in each season in Oyster Harbour (Fig. 8). In Irwin Inlet, catch rates in winter declined markedly in the river but not in the basin (Fig. 8), thereby paralleling the situation with species richness (cf Fig. 7) and largely accounting for the significant estuary × region × season interaction. The small region × year × season interaction in the rivers can be largely attributed to the mean catch rates being particularly low in the rivers in winter 2006 and high in autumn 2007 and especially so in Irwin Inlet (data not shown).

In Wellstead Estuary, three-way ANOVA demonstrated that species richness differed significantly between region and season, with the mean square and significance level being far higher for region (Table 8). Mean species richness ranged from 5.3 in autumn to 7.1 in winter in the basin and from 2.6 in summer to 4.3 in autumn in the river. Catch rate was significantly influenced by season and there were significant region × year and year × season interactions, with the mean square and significance level being highest for the region × year interaction (Table 8). The mean catch rate in the river was greater than in the basin in 2006, i.e. 85 vs 67 fishes h^{-1}, whereas the reverse was the case in 2007, i.e. 49 vs 95 fishes h^{-1}.

Table 6
R statistic values and significance levels for two-way ANOSIMs for year and season derived from the matrices constructed using percentage contributions of the various fish species to the ichthyofaunal compositions in replicate samples from the basin and river of Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Estuary	Basins		Rivers	
	Year	Season	Year	Season
Broke Inlet	0.149**	0.291***	0.046	−0.034
Irwin Inlet	0.293***	0.349***	0.250	0.259**
Wilson Inlet	0.022	0.090**	−0.046	0.071
Oyster Harbour	0.018	0.137**	−0.102	−0.140
Wellstead Estuary	0.297***	0.100*	0.528**	0.398**

4. Discussion

This paper provides the first quantitative data on the ichthyofaunal compositions of offshore, deeper waters in the basins and rivers of permanently-open, seasonally-open and normally-closed estuaries along the same coast and which have been based on seasonal sampling of the same sites over successive years. Our study has enabled the species compositions, contributions of different life-cycle guilds, species richness and catch rates in estuaries with divergent environmental characteristics to be compared. They have thus allowed the ways in which factors related to the "status" of the estuary mouth, the region within estuary and the time of year influence the characteristics of the ichthyofaunas of offshore waters

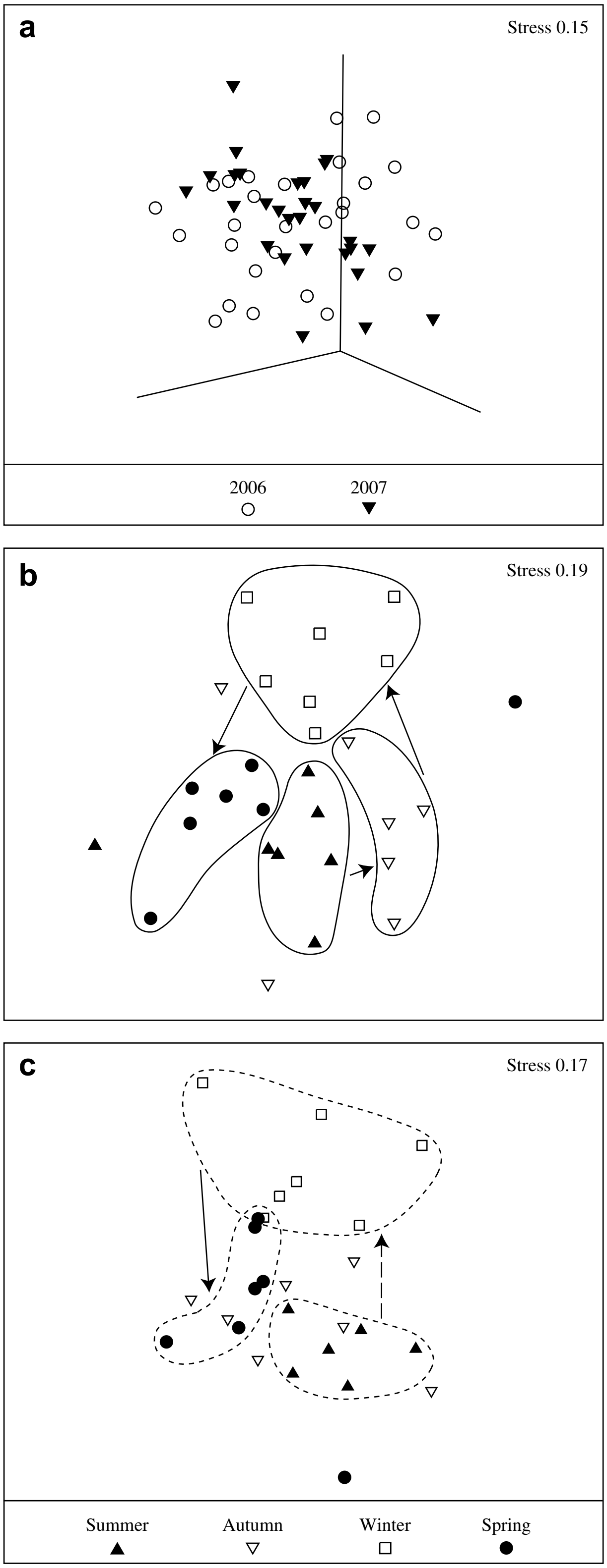

Fig. 5. Non-metric multidimensional scaling ordination plots of the matrices derived from the percentage contributions of each species to replicate samples obtained in offshore, deeper waters of the basin of Irwin Inlet in each season of a) 2006 and 2007, b) each season of 2006 and c) each season of 2007. NB. In c) an extreme outlying summer sample has been excluded from the ordination plot.

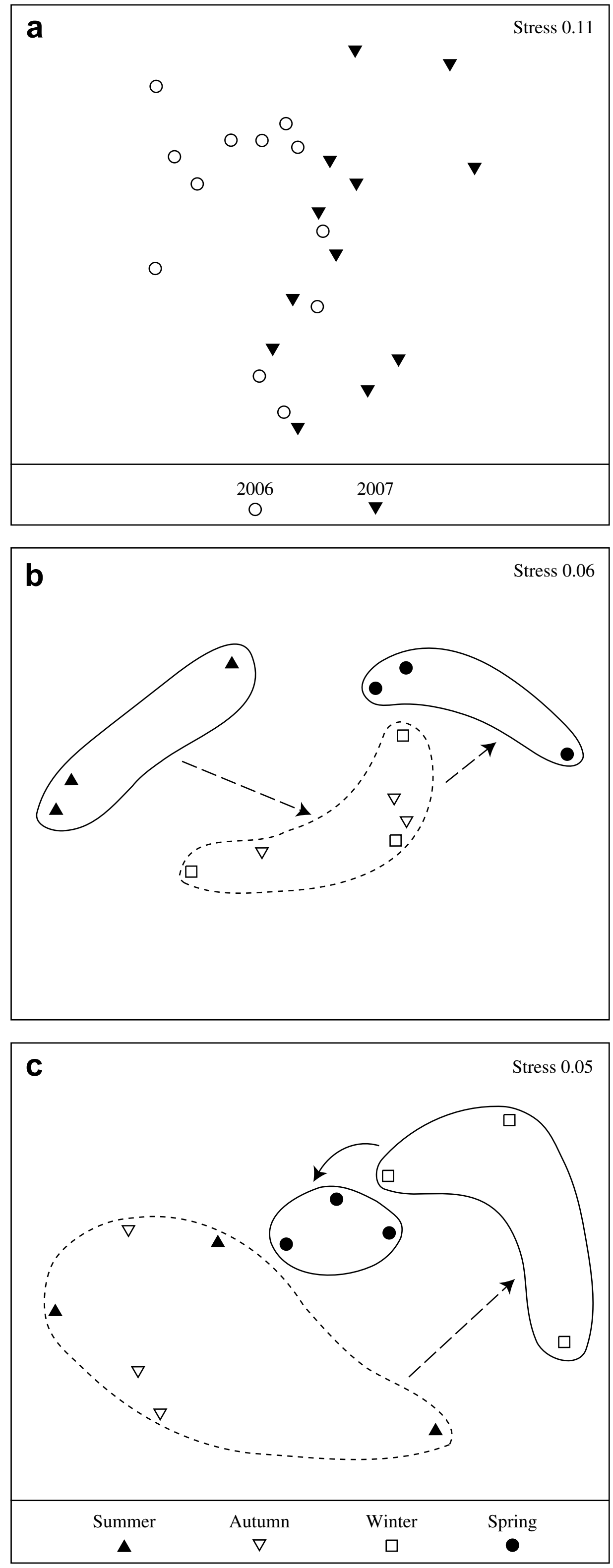

Fig. 6. Non-metric multidimensional scaling ordination plots of the matrices derived from the percentage contributions of each species to replicate samples in offshore, deeper waters of the river of Wellstead Estuary in a) each season of 2006 and 2007, b) each season of 2006 and c) each season of 2007.

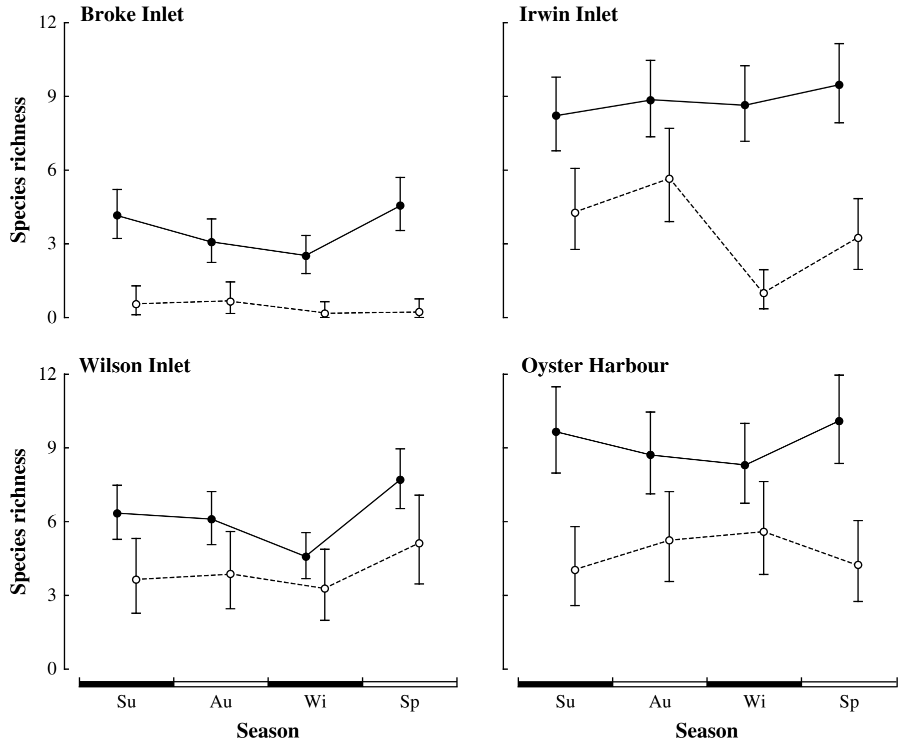

Fig. 7. Mean species richness ±95% CI derived from back-calculated data for offshore, deeper waters of the basin (solid line) and river (dashed line) of Broke, Irwin and Wilson inlets and Oyster Harbour in each season.

of microtidal estuaries to be elucidated. The clarification of the roles of such factors is particularly important as many estuaries are becoming highly degraded and/or modified (e.g. McComb, 1995; Jackson et al., 2001), and yet still act as important nursery areas for marine fish species and frequently support important recreational and commercial fisheries (e.g. Haedrich and Hall, 1976; Lenanton and Potter, 1987; Whitfield, 1998; Blaber et al., 2000).

4.1. Relationships between contributions of life-cycle guild and estuary type

The estuaries of temperate regions of the northern hemisphere, which are typically permanently-open and macrotidal, are dominated by marine species and particularly by their juveniles (Haedrich, 1983; Claridge et al., 1986; Elliott and Dewailly, 1995). The paucity of estuarine-spawning species in these estuaries presumably reflects, in part, the fact that the turbulent and turbid conditions in these tidally-dominated systems are not particularly conducive to the survival of the eggs and larvae of many fish species. Because rainfall and thus discharge is very low in the late spring to early autumn in south-western Australia and tidal action in the estuaries of this region is very limited, the conditions in these systems are far more benign during the period when many estuarine-spawning fish species breed (Potter and Hyndes, 1999). While this would account for the success of such species in south-western Australian estuaries and particularly amongst the small species, such as those of the Atherindae and Gobiidae, which are found in shallow, nearshore waters, other estuarine-spawning species, such as *Acanthopagrus butcheri*, *Cnidoglanis macrocephalus* and *Engraulis australis*, which were caught during the present study, are abundant in the offshore, deeper waters of these estuaries.

The marked differences between the contributions of the number of species representing the different life-cycle guilds to the ichthyofaunas of offshore, deeper waters of five estuaries on the south coast of Western Australia can be related to differences in estuary type. Thus, for example, while 21 species of marine straggler and 18 species of marine migrant were caught in the permanently-open Oyster Harbour, only 1 species of marine straggler and 9 species of marine migrant were recorded in the normally-closed Wellstead Estuary. Furthermore, the numbers of species representing these two guilds collectively in the seasonally-open Broke, Irwin and Wilson inlets ranged from 21 to 25 and were thus intermediate. These findings largely parallel those recorded for comparable types of estuaries in southern Africa, which likewise frequently contain narrow mouths that can become closed though the formation of sand bars (Bennett, 1989; Whitfield and Kok, 1992; Vorwerk et al., 2003; Harrison and Whitfield, 2006). As many marine species did not penetrate the saline reaches of the rivers,

Table 7
Mean squares and significance levels for four-way ANOVAs of the numbers of species and catch rates of fishes at sites in the basins and rivers of offshore, deeper waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary in each season of 2006 and 2007. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Main effects					
	Estuary (E)	Region (R)	Year (Y)	Season (S)		Residual
df	3	1	1	3		278
Number of species	24.711***	60.584***	0.631	1.607***		0.247
Catch rate	24.368***	3.804***	3.728***	0.979*		0.340
	Two-way interactions					
	E × R	E × Y	E × S	R × Y	R × S	Y × S
df	3	3	9	1	3	3
Number of species	2.197***	0.252	0.424	0.036	0.642	0.080
Catch rate	7.711***	0.381	0.548	0.428	1.610**	0.944*
	Three- and four-way interactions					
	E × R × Y	E × R × S	E × Y × S	R × Y × S		E × R × Y × S
df	3	9	9	3		9
Number of species	0.354	0.568*	0.344	0.303		0.090
Catch rate	0.707	0.939**	0.515	1.090*		0.319

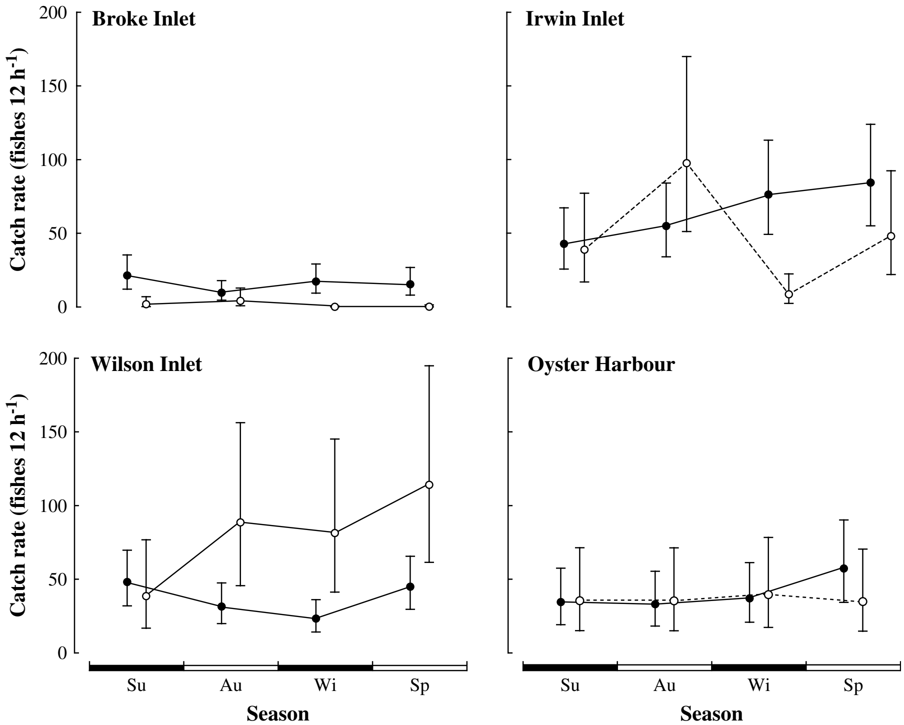

Fig. 8. Mean catch rate ±95% CI derived from back-calculated data for offshore, deeper waters of the basin (solid line) and river (dashed line) of Broke, Irwin and Wilson inlets and Oyster Harbour in each season.

the above trends between numbers of marine species and estuary type largely reflect the situation in the basins.

The relationships between the contributions made by the number of individuals of marine species and estuary type did not always follow the same trend as species richness. Thus, for example, although Oyster Harbour is permanently open and Wellstead Estuary is normally closed, the contributions made by the number of individuals of marine species to the total catch were similarly high in both their basins, i.e. 79 and 73%, respectively, and their rivers, i.e. 50 and 45%, respectively. However, whereas the high contribution in Oyster Harbour was due to appreciable catches of a number of marine species, that in Wellstead Estuary was mainly attributable to the presence of substantial numbers of *Mugil cephalus* and *Aldrichetta forsteri* and to the very low abundances of estuarine-spawning species other than *Acanthopagrus butcheri*. Marine species presumably entered Wellstead Estuary in the period immediately prior to and after the commencement of the study when the estuary was open to the ocean, and were subsequently prevented from emigrating from the estuary through its closure for the rest of the study.

The contribution of marine species to the total catch in the basin of Wilson Inlet was the lowest by far of any estuary (57.8%), which was partly due to the estuary mouth being closed for much of the study and, even when the sand bar had been breached, the opening was small and thereby reduced the opportunities for immigration from the sea. However, it also reflects the presence of large numbers of estuarine residents, such as *Engraulis australis*, *Cnidoglanis macrocephalus* and *Platycephalus speculator*, which collectively made a particularly large contribution to the ichthyofauna of the basin of this estuary, as was also the case in 1987–1989 (Potter et al., 1993).

The high contributions (>75%) made by marine migrants to the total catches in both the basins and rivers of Irwin and Broke inlets reflected the immigration of substantial numbers of *Aldrichetta forsteri*, *Arripis georgianus* and *Mugil cephalus* at times when the mouths of those estuaries were open and allowed good exchange between the ocean and the estuary. However, they also reflect the relatively low overall abundance of estuarine-spawning species and particularly of *Acanthopagrus butcheri*, which was very abundant in each of the other estuaries.

4.2. Ichthyofaunal compositions of the rivers

Our data demonstrate conclusively that there is a major overarching difference between the ichthyofaunal compositions of the basins and rivers across all estuaries and which does not thus depend on whether an estuary is permanently open, seasonally open or normally closed. Indeed, the distinction between the ichthyofaunal compositions of the basins and rivers is greater than that of the overall difference between the compositions in the five estuaries. It is therefore particularly relevant that the riverine ichthyofaunas were always characterised predominantly by consistently large numbers of *Mugil cephalus* and also of *Acanthopagrus butcheri* in all estuaries except Broke Inlet. The marine species *M. cephalus* is likewise abundant in many estuaries

Table 8
Mean squares and significance levels for three-way ANOVAs of the number of species and catch rate of fish recorded at sites in the basins and rivers of offshore, deeper waters of Wellstead Estuary in each season of 2006 and 2007. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Main effects			
	Region (R)	Year (Y)	Season (S)	Residual
df	1	1	3	48
Number of Species	4.990***	0.031	0.311*	0.091
Catch rate	0.339	0.061	0.489**	0.110
	Two- and three-way interactions			
	R × Y	R × S	Y × S	R × Y × S
df	1	3	3	3
Number of Species	0.064	0.223	0.209	0.066
Catch rate	1.585***	0.297	0.421*	0.186

throughout its wide distribution and penetrates far upstream in these systems and even into freshwater (Thomson, 1957a; Blaber and Whitfield, 1977; Chubb et al., 1981; Cardona, 2000). The estuarine resident *A. butcheri* also has a marked tendency to occupy the river region of other estuaries, particularly during the dry late spring to autumn months, and to spawn in that region (Sarre and Potter, 1999). The overwhelming importance of *M. cephalus* and *A. butcheri* to the ichthyofaunas of the rivers is emphasised by the fact that the only other species to rank in the top two typifying species for the river of any estuary was *Argyrosomus japonicus* in Oyster Harbour.

Although *Mugil cephalus* was of overriding importance in characterising the fish faunas of the rivers of each estuary, and the same was true for *Acanthopagrus butcheri* in all estuaries except Broke Inlet, the compositions of the fish faunas in the rivers of the various estuaries were significantly different. These differences thus reflect, in particular, variations in the contributions of *M. cephalus* and usually also *A. butcheri* to the fish faunas of the rivers, recognising that the distinction between the fish faunas of the rivers of Wilson Inlet and Wellstead Estuary was far less than between the rivers of all other pairs of estuaries. In the case of the river of Oyster Harbour, however, the composition of its ichthyofauna was discrete, largely due to the unique and substantial contribution made by juvenile *Argyrosomus japonicus*, indicating that this marine sciaenid spawns nearby.

The capture of only two *Acanthopagrus butcheri* in the river of Broke Inlet is remarkable in that this sparid is not only abundant in the rivers of the other four estuaries, but also typically in other south-western Australian estuaries (Potter and Hyndes, 1999). The paucity of *A. butcheri* in the river of Broke Inlet parallels the situation recorded in the 1970s and 1980s by Hodgkin and Clarke (1989), who attributed this phenomenon to the very low salinities present in that river during winter. A combination of the very low catches of *A. butcheri* and relatively low catches of *M. cephalus* in the river of Broke Inlet, the only typifying species for this estuarine region, explains why, in each season of the two years, the overall catch rate was far lower in the river of this estuary than in that of any other estuary.

4.3. Ichthyofaunal compositions of the basins

The contrast between the overriding importance of one or generally both of *Mugil cephalus* and *Acanthopagrus butcheri* to the ichthyofaunas of the river of each estuary and their greatly reduced importance in the basins of those estuaries clearly contributed greatly to the overall distinction between the ichthyofaunal compositions of these two major regions in estuaries. In contrast to the rivers, the major typifying species for the ichthyofaunas varied far more markedly among the basins, with *Aldrichetta forsteri* and *Arripis georgianus* being the only two species to play this role in more than two estuaries. As substantial numbers of both *A. forsteri* and *A. georgianus* were caught below and above their respective lengths at maturity (Thomson, 1957b; Fairclough et al., 2000), these estuaries provide an important environment for both the juveniles and adults of these marine species on the south coast of Western Australia. The only other species to act as a typifying species for the ichthyofauna of the basin of more than one estuary was the estuarine resident *Cnidoglanis macrocephalus,* which performed this function in both Irwin and Wilson inlets. Furthermore, several species acted as major typifying species of the ichthyofauna of only one estuary. The far greater variation among the typifying species of the basins than rivers helps explain why the differences among ichthyofaunal compositions are almost invariably greater among basins than rivers.

The marked differences among the ichthyofaunal compositions in the basins of the various estuaries on the south coast of Western Australia contrast with the conclusions derived from analysing samples collected by gill netting in 10 either permanently- or intermittently-open estuaries in southern Africa (Vorwerk et al., 2003). The differences in our study are attributable to variations in the duration over which those estuaries were connected to the ocean and/or the types of environment found within the basins. Thus, for example, ichthyofaunal composition in the basin of the estuary that remained permanently open to the sea, and thus in which salinity remained close to that of full-strength sea water, i.e. Oyster Harbour, was the most discrete of any of the basins, reflecting, in particular, the immigration of a diverse range of marine species (see Section 4.1 for further discussion of influence of status of estuary mouth). In the context of environmental conditions, it is relevant that, as detached macrophytes constitute an important nursery habitat for *Cnidoglanis macrocephalus* (Crawley et al., 2006), this plotosid was most abundant in the basin of Irwin and Wilson inlets in which the growths of the seagrass *Ruppia megacarpa* were very prolific. The paucity of macrophyte growth in Broke Inlet could thus help account for the absence of this plotosid from the basin of this estuary.

The relatively far larger contribution made by *A. butcheri* to the ichthyofauna of the basin of Wellstead Estuary than to that of this region in any other estuary almost certainly reflects the fact that the morphological and environmental distinction between basin and river and thus their habitats is the least marked of any estuary (Fig. 1). This conclusion is consistent with the difference between the ichthyofaunal compositions of the basins and rivers being least in Wellstead Estuary.

4.4. Temporal variations in ichthyofaunal compositions

Ichthyofaunal composition was found only occasionally to undergo clear interannual or seasonal changes in either the basins or rivers of the five estuaries. The greatest interannual shift in the ichthyofaunal composition occurred in the river of Wellstead Estuary and this was accompanied by lesser but still significant changes to the ichthyofauna of the basin. It is thus relevant that the Wellstead Estuary became closed to the sea early in the study and remained so for the rest of its duration. The interannual shift in this river was attributable, in particular, to a marked increase in the relative abundances of both *Mugil cephalus* and *Aldrichetta forsteri* in the gill net catches. Comparisons between length-frequency data for sequential seasonal seine and gill net samples from nearshore, shallow and offshore, deeper water, respectively, demonstrate that the interannual changes can be explained by the following sequence of events. Substantial numbers of the small juveniles of the above two species of marine mugilid were recruited into the nearshore waters of this estuary immediately prior to and just after the commencement of the study, when the estuary mouth was open, and then, as they increased in size, moved offshore and became susceptible to capture by gill netting during the second year of the study. As the closure of the mouth of Wellstead Estuary resulted in the salinity in each season of the second year exceeding that of the corresponding season in the first year of the study, the overall increase in salinity to levels appreciably above that of sea water may have had a differential effect on the various species and thus also contributed to the shift in species composition between years.

The greatest seasonal changes in ichthyofaunal composition in the basins occurred in those of the Irwin and Broke inlets, which underwent the greatest intra-annual changes in salinity. Although ichthyofaunal composition also underwent pronounced seasonal changes in the river of Irwin Inlet, this was not the case in the river of Broke Inlet, in which the ichthyofauna was highly depauperate. The pronounced cyclical changes that occurred in the basin of Irwin Inlet in each year reflected, inter alia, increased abundances of

Aldrichetta forsteri in summer and autumn, of *Arripis georgianus* in summer, autumn and spring and of *Mugil cephalus* in winter. These changes reflect a combination of differences in the movement patterns of the various fish species into and out of the basin when the estuary mouth was open and into and out of the rivers during periods of low and high freshwater discharge, respectively. Cyclical changes in ichthyofaunal composition in permanently-open estuaries have been related to the time-staggered immigrations and emigrations of various fish species in both macrotidal (Claridge et al., 1986; Potter et al., 1986; Maes et al., 2005) and microtidal estuaries (Young and Potter, 2003a; Hoeksema and Potter, 2006). The seasonal changes in the river of Wellstead Estuary, and particularly in the first year, were far less cyclical than in the basins of Irwin and Broke inlets, presumably reflecting the fact that the environment of this system changed during the study as a result of the estuary mouth shifting from being open at the very beginning of the study to being closed for all of the remaining period.

4.5. Species richness and catch rates: inter- and intra-estuarine comparisons

Our finding that the mean species richness in each estuary was greater in its basin than river was largely attributable to the fact that many of the marine species found in the basins, including all of the marine stragglers, never penetrated the rivers, presumably representing, at least in part, a preference for higher salinities. Furthermore, although always relatively low, the number of estuarine-spawning species was always greater in the basin than river of each estuary. This is consistent with south-western Australian estuaries being of recent origin (Hodgkin and Hesp, 1998) and that such fish populations were probably derived from those found in the marine environment and thus, as with marine stragglers, they presumably prefer salinities closer to those of full-strength sea water.

In contrast to the situation with species richness, the catch rates showed no consistent trend to be greater in the basins than rivers across all estuaries. Indeed, in the Wellstead Estuary, they were greater in the river than basin in 2006 and vice versa in 2007. The large 95% confidence limits for several of the mean seasonal catch rates, and particularly for some of those in the rivers, reflected variability in the catches of certain species through their tendency to form aggregations in certain areas, e.g. *Mugil cephalus* (Major, 1978; Chubb et al., 1981) and *A. butcheri* (Sarre and Potter, 1999), and thus to vary in density among sampling sites within a region of the estuary at any given time.

It was conspicuous that, in each season, the mean catch rates in both the basin and river of Broke Inlet were lower than in the corresponding regions of Irwin and Wilson inlets and Oyster Harbour. This finding is consistent with Broke Inlet being by far the most oligotrophic of those four systems (Hodgkin and Clarke, 1989) and therefore containing the least amount of food for those invertebrates that constitute the prey of most fish species and providing the least macrophyte cover for fishes. In contrast, the overall abundance of fishes was greatest in Wellstead Estuary, which is eutrophic and has high primary productivity (Brearley, 2005). Elsewhere in south-western Australia, an increase in eutrophication in the large Peel-Harvey Estuary over time resulted in an increase in the catch per unit of effort for the commercial fishery and thus presumably in the overall abundance of fishes (Steckis et al., 1995). Furthermore, a subsequent decline in eutrophication in that same estuary was accompanied by a marked reduction in the overall abundance of fishes (Young and Potter, 2003b).

In summary, this study emphasises that the characteristics of the ichthyofaunas of offshore, deeper waters of the basins and rivers of microtidal estuaries are very different, irrespective of whether the estuary is permanently open, seasonally open or normally closed. Indeed, the overall differences in the ichthyofaunal compositions of those two regions were even greater than amongst these divergent estuaries as a whole. This emphasises that it is crucial to take into account the region of estuary, when making overall comparisons between estuaries in which there are marked differences between the environmental characteristics of their main regions, such as is often found in microtidal temperate regions. Although the typifying species for the rivers were essentially the same in all estuaries, those for the basins varied among these systems, reflecting, in particular, the influence of differences in the status of the estuary mouth and types of habitat present. Species richness and catch rates were least in the most oligotrophic estuary and catch rates were particularly high in an estuary that was highly eutrophic.

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