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Ichthyofaunas of a temperate estuary and adjacent marine embayment. Implications regarding choice of nursery area and influence of environmental changes

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Abstract A fine-mesh seine net was used at regular intervals to collect fishes from the entrance channel and basin of the Blackwood River Estuary (south-western Australia), from Deadwater Lagoon, which is joined to the entrance channel by a narrow and shallow watercourse and thus constitutes part of this estuary, and from Flinders Bay into which the estuary discharges. Sampling was at six-weekly intervals between February and December 1994. The juveniles of some marine species, such as *Pelates sexlineatus*, *Rhabdosargus sarba* and *Aldrichetta forsteri*, were either found only in the estuary or were in far higher densities in the estuary than in Flinders Bay. In contrast, the juveniles of some other marine species, such as *Sillago schomburgkii*, were relatively abundant in both environments, while others such as *S. bassensis*, *Pelsartia humeralis*, *Lesueurina platycephala* and *Spratelloides robustus* were either far more abundant in Flinders Bay or entirely restricted to this marine embayment. The various marine species found in inshore waters thus apparently vary considerably in their "preference" for estuaries as nursery areas. Although some marine species were abundant in the shallows of the estuary, the fish fauna of these waters was dominated by the estuarine-spawning species *Leptatherina wallacei*, *Favonigobius lateralis*, *L. presbyteroides* and *Atherinosoma elongata*. The above regional differences help account for the very marked difference that was found between the compositions of the shallow-water ichthyofaunas of Flinders Bay and each of the three estuarine regions. The ichthyofaunal compositions of the basin and channel underwent pronounced changes during winter, when freshwater discharge increased markedly and salinities in the estuary thus declined precipitously. This faunal change was mainly attributable to the emigration of marine stragglers, a reduction in the densities of marine estuarine-opportunist species such as *Pelates sexlineatus* and *R. sarba*, and the immigration of large numbers of both young 0+ *Aldrichetti forsteri* from the sea and of *L. wallacei* from the river. Although most of the above species were also abundant in Deadwater Lagoon, the ichthyofaunal composition of this region did not undergo the same seasonal changes, presumably due to the lack of riverine input and thus the maintenance of relatively high salinities throughout the year. The number of marine straggler species was much lower in Deadwater Lagoon than in the estuary basin, reflecting a far more restricted tidal exchange with the entrance channel. However, the overall density of fishes was far higher in Deadwater Lagoon than in the estuary basin or entrance channel, due mainly to the far higher densities of the estuarine species *Atherinosoma elongata* and *L. wallacei* and of the 0+ age class of the marine species *R. sarba.* The high densities of certain species in Deadwater Lagoon are assumed to be related, at least in part, to the high level of productivity and protection that is provided by the presence of patches of *Ruppia megacarpa*, an aquatic angiosperm that was not present in the estuary basin or entrance channel.

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Introduction

The shallow waters of estuaries act as important nursery areas for a number of marine species of teleost in both the northern and southern hemispheres (Blaber and Blaber 1980; Haedrich 1983; Kennish 1990; Potter et al. 1990). The marine fish species that use estuaries as nursery areas, termed marine estuarine-opportunists, can be contrasted with the marine stragglers, which are typically found irregularly and in low numbers near the mouths of estuaries (Lenanton and Potter 1987). Although relatively few fish species complete their life cycles in estuaries in the temperate regions of the northern hemisphere (Kennish 1990), such species do make a substantial contribution to the overall abundance of fishes in the estuaries of south-western Australia and southern Africa (Potter et al. 1990).

The value of estuaries to the juveniles of euryhaline marine teleosts resides in the fact that they are sheltered and highly productive ecosystems and contain relatively few large piscivorous predators (Cronin and Mansueti 1971; Haedrich 1983; Claridge et al. 1986; Kennish 1990). The overall productivity of estuaries is often enhanced by the presence of vegetated areas, which provide an important source of food and cover for small fish (Kikuchi 1980; Bell and Pollard 1989; Humphries et al. 1992). The nearshore waters of marine embayments, which also provide an abundance of food and protection from predation, often act as alternative or the main nursery areas for certain marine estuarine-opportunistic species of teleosts (Lenanton 1982; Clark et al. 1994; Blaber et al. 1995). However, no study has compared concurrently the composition of the fish faunas of the shallows throughout estuary with those in nearby, protected marine waters with the specific objective of ascertaining the relative roles of these two habitat types as nursery areas for the various species of marine fishes found in the same region.

The Blackwood River Estuary, which is a permanently open system located at the extreme south-western corner of Australia, comprises a large and shallow central basin, which is supplied by a long river and opens into the marine waters of Flinders Bay through a narrow entrance channel (Fig. 1). This morphological arrangement is typical of many estuaries in southern Australia and southern Africa (Day 1981; Hodgkin and Lenanton 1981; Potter et al. 1990). However, the Blackwood River Estuary is unusual in that a "lagoon" (Deadwater) is connected to the entrance channel of this estuary. Deadwater Lagoon receives no direct riverine input and, unlike other areas within and outside the estuary, contains patches of the aquatic angiosperm *Ruppia megacarpa*. Since the Blackwood River Estuary is located in an area of high but very seasonal rainfall (Hodgkin 1978), the amount of freshwater discharge undergoes pronounced seasonal changes, thereby producing marked changes in the salinity regime in the estuary basin and channel (Lenanton 1977; Hodgkin 1978).

The present study compares the compositions of the ichthyofaunas in the shallows of Flinders Bay with those of the shallows of different regions of the Blackwood River Estuary, thereby enabling us to ascertain the relative degree to which the marine species in the region apparently have a "preference" for using estuaries as a nursery area. The presence of two basin-like areas within the Blackwood River Estuary, both of which open into the entrance channel but only one of which has a riverine input, has also enabled us to determine whether the marked increase in freshwater discharge and consequent decline in salinity that occurs in winter have a marked influence on ichthyofaunal composition and, if so, which species are most affected. Finally, we have tested the hypothesis that, since Deadwater Lagoon is closer to the estuary mouth than the estuary basin and, in contrast to the estuary basin, contains numerous patches of *Ruppia megacarpa* and thus a greater amount of food, protection and structural heterogeneity, it will house a greater number of fish species and a greater overall abundance of fishes.

Materials and methods

The basin of the Blackwood River Estuary has an area of ~9 km^2 and is generally <2 m in depth, while the entrance channel is 3 km long and 0.5 km wide and in several places exceeds 3 m in depth (Fig. 1). Deadwater Lagoon, which is mostly <2 m depth, is joined to the entrance channel near the mouth of the estuary and, for the purposes of this study, is considered to be a region of the estuary (Fig. 1).

Fishes in 12 shallow-water sites (depth <1.5 m) (3 from each region) in the estuary basin, entrance channel, Deadwater Lagoon and relatively protected areas of Flinders Bay (Fig. 1), were sampled using a seine net during both the day and night at six-weekly intervals between February and December 1994. Salinity and temperature were recorded in the middle of the water column at each site on each sampling occasion. The seine net, which was 21.5 m long, consisted of 10 m-long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m bunt made of 3 mm mesh. The net had a drop of 1.5 m and swept an area of 116 m^2.

The total number of individuals of each species in each sample was recorded. [Note: the relative compositions of the various species recorded in our study cannot be compared directly with those

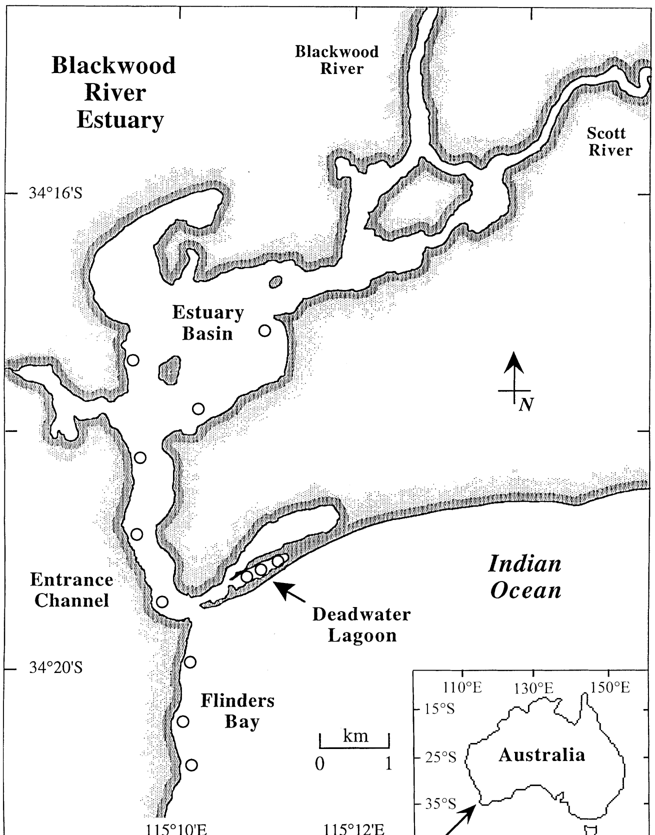

Fig. 1 Positions (○) of the 12 sampling sites (3 in each region) in estuary basin, entrance channel and Deadwater Lagoon regions of Blackwood River Estuary and in Flinders Bay (*Inset* arrow shows location of Blackwood River Estuary in Australia)

recorded during a survey of the fish fauna of the Blackwood River Estuary carried out 20 yr earlier by Lenanton (1977) since, in that study, a far larger mesh was used in both the wings (maximum mesh sizes of 25 vs 9 mm), and in the pocket (9.5 vs 3 mm), which would have meant that many small fishes would have escaped. Furthermore, at that time, the atherinid species, which are very abundant in south-western Australian estuaries (Potter et al. 1990), had not yet been adequately described (Prince et al. 1982).] The total length of each fish was measured to the nearest 1 mm, except when the number of a species was large, in which case the lengths of a random sample of 100 fish of that species were recorded. On the basis of detailed studies of the biology of fish species in south-western Australian estuaries, each of the species caught in these estuaries has been categorised as either a marine straggler (S), marine estuarine-opportunist (O) or estuarine-spawning species, the latter formerly being designated collectively as estuarine (E) (see Potter et al. 1990, 1993). However, in this paper, the latter category has been separated into those species which typically spawn only in estuaries (E) and species which can spawn in both estuarine and marine environments (E/M). Those marine species that were caught in Flinders Bay, and have never been recorded in estuaries in south-western Australia, have been termed solely marine (SM).

The number of individuals of each species in each of the samples from each region has been expressed as a density, i.e. number of fish 100 m^{-2}. A three-way analysis of variance (ANOVA) was used to determine whether the number of fish species, the overall density of fishes and the densities of the five most consistently abundant fish species differed significantly among regions, months and time of day, i.e. day or night. Since Cochran's *C*-test showed that the densities of fishes were heteroscedastic, they were each $\log_{10}(n+1)$-transformed, which usually resulted in homoscedasticity and therefore satisfied the assumptions of ANOVA. All factors in the above analyses were considered fixed. When ANOVA showed a significant difference, the a posteriori Scheffé's test was used to determine which means were significantly different at the 0.05 probability level. Emphasis is placed on those effects which have high and significant mean squares in the ANOVAs. Although the interactions for region × month were often significant, their mean squares were usually relatively low and were thus less important than one or more of the main effects.

The mean densities of each species sampled during the day and night in each of the three regions of the Blackwood River Estuary and in a region of Flinders Bay just outside the estuary, were classified by hierarchical agglomerative clustering using group-average linking, and ordinated using the multidimensional scaling techniques in the PRIMER package (Clarke and Warwick 1994). Prior to classification and ordination, the densities were root-root transformed and the Bray–Curtis similarity measure was used to produce the association matrix. Analysis of similarities (ANOSIM) was used to test whether the compositions of the ichthyofaunas in the different regions were significantly different, while similarity of percentages (SIMPER) was employed to ascertain the species most responsible for the Bray–Curtis dissimilarity between groups (Clarke 1993). Multivariate dispersion (MVDISP) was used to determine the degree of dispersion of the samples in the four regions during both day and night (Somerfield and Clarke 1997).

Between May 1994 and January 1995, sampling was also carried out in each of the four seasons during the day, using the same seine net as described above in nearby sand and dense *Ruppia megacarpa* habitats at each of three sites in Deadwater Lagoon. Since there had previously been a detailed study of the distribution of the atherinids and gobiids of these two extreme habitat types in the nearby Wilson Inlet (Humphries et al. 1992), the present study has focused on marine estuarine-opportunists, which were not abundant in that other south-western Australian estuary (Potter et al. 1993).

Results

Salinity and temperature

Since the mean salinities and water temperatures at the three sites in each region were almost invariably similar during the day and night, the data for these two variables during the day and night in each region have been pooled. Mean monthly salinities in the Blackwood River Estuary varied markedly between regions and months (Fig. 2). Salinities in the basin and channel remained above ~25‰ until May, but then started to decline precipitously in June, eventually reaching a minimum of ~2 and 4‰, respectively, in July. Salinities remained low in these two regions until September, after which they rose sharply, reaching ~29‰ in the basin and 32‰ in the channel in December (Fig. 2). Although salinities in Deadwater Lagoon remained above 28‰ for most of the year, they did decline to ~23‰ in July (Fig. 2). Salinities in Flinders Bay remained above 31‰ in all months except March, when they declined to ~29‰ (Fig. 2).

The trends shown by the mean monthly temperatures in the basin and channel were very similar, with values reaching relatively high levels of ~24 °C in March, be-

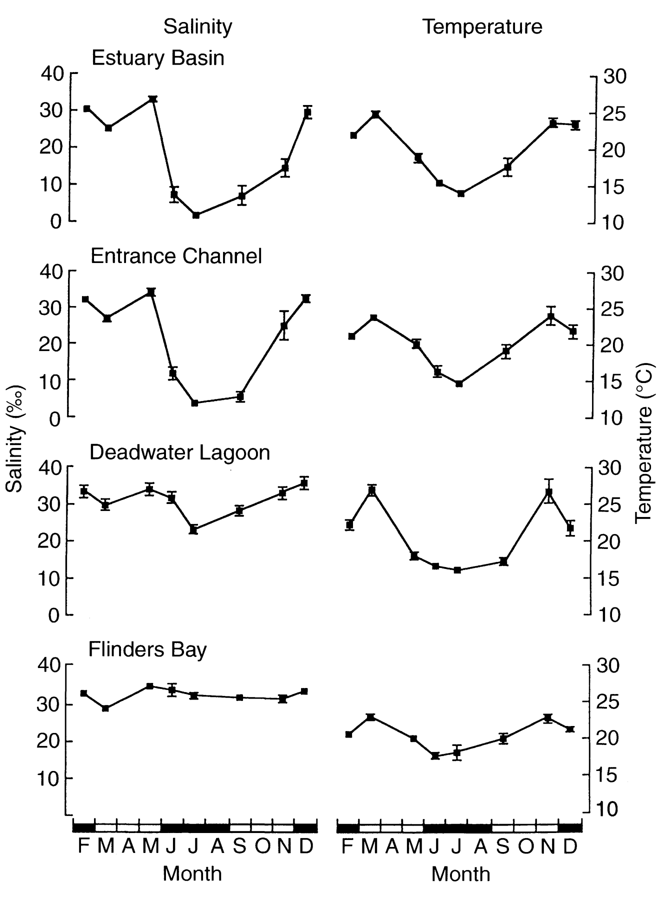

Fig. 2 Mean salinities and temperatures ± 1 SE in middle of water column at sampling sites in estuary basin, entrance channel and Deadwater Lagoon of Blackwood River Estuary and in Flinders Bay between February and December 1994 (*Black rectangles and open rectangles on x-axis* summer and winter months, and spring and autumn months, respectively)

fore declining progressively to a minimum of ~14 °C in July. Temperatures in both regions then increased to ~24 °C in November (Fig. 2). In Deadwater Lagoon, temperatures reached a peak of ~27 °C during March, and then decreased markedly to ~17 °C in May and remained at about this level over the ensuing months, before rising sharply to ~27 °C in November (Fig. 2). Although temperatures followed the same seasonal trends in Flinders Bay as in each region of the estuary, they ranged only from ~18 to 23 °C (Fig. 2).

Faunal composition

Between February and December 1994, a total of 63 587 fishes, representing 49 species, were collected by seine net from the shallows of the estuary basin, entrance channel and Deadwater Lagoon of the Blackwood River Estuary, and from Flinders Bay (Table 1). This corresponded to a total of 54 816 fishes, after the numbers of fishes in each sample in each region had been adjusted to an area of 100 m^2 (Table 1). The numbers of species recorded in the estuary basin and entrance channel, i.e. 31 and 34, respectively, were greater than the 23 collected in Deadwater Lagoon and the 26 caught in Flinders Bay. However, the total number of fishes caught in Deadwater Lagoon, i.e. 25 021, was far greater than in both the estuary basin and entrance channel, i.e. 10 031 and 16 654, respectively, and more than eight times the 3 110 obtained in Flinders Bay (Table 1).

While the suites of the relatively most abundant species, i.e. those that typically contributed >1% to the total number of fishes, were similar in the estuary basin, entrance channel and Deadwater Lagoon, they each differed markedly from that in Flinders Bay (Table 1). Thus, in terms of relative abundance, the same nine species were the most numerous species in both the estuary basin and entrance channel, and eight of these were amongst the nine most numerous species in Deadwater Lagoon, whereas only two of these species ranked amongst the nine most abundant species in Flinders Bay. In terms of ranking by abundance, the species sequence was more similar between the estuary basin and entrance channel than between either of these regions and Deadwater Lagoon. The most abundant species in the estuary basin and entrance channel included the estuarine species *Leptatherina wallacei*, *Afurcagobius suppositus*, *Atherinosoma elongata*, and *Pseudogobius olorum*, the estuarine/marine species *Favonigobius lateralis* and *L. presbyteroides*, and the marine estuarine-opportunists *Pelates sexlineatus*, *Rhabdosargus sarba* and *Aldrichetta forsteri* (Table 1). With the exception of *P. sexlineatus* and, more particularly *Afurcagobius suppositus*, the above species were also relatively abundant in Deadwater Lagoon. However, the marine estuarine-opportunist *Sillaginodes punctata* was more abundant in Deadwater Lagoon than in either the estuary basin or entrance channel. The only two species which ranked among the most abundant in the estuary basin, entrance channel and Deadwater Lagoon and had a similar high ranking in Flinders Bay, were *L. presbyteroides* and *Aldrichetta forsteri*. However, reasonable numbers of *Sillago schomburgkii* were caught in both the estuary and Flinders Bay.

The fauna in Flinders Bay was so dominated by *Leptatherina presbyteroides* that this species contributed over three-quarters of the total number of fishes collected from the shallows of that marine embayment. However, the total catch of this species was still very much lower in Flinders Bay than in both the entrance channel and Deadwater Lagoon (Table 1). The catches of *L. presbyteroides* in the entrance channel and Deadwater Lagoon, as well as in Flinders Bay, were far greater than in the estuary basin (Table 1). Other species that made a substantial contribution to the total catch in Flinders Bay included the strictly marine or marine straggler species *Spratelloides robustus*, *Sillago bassensis*, *Pelsartia humeralis*, *Lesueurina platycephala* and the marine estuarine-opportunists *Aldrichetta forsteri* and *Sillago schomburgkii*, and the estuarine/marine species *Cnidoglanis macrocephalus*. With the exception of *A. forsteri*, the above species were either not caught, or were caught only in very small numbers inside the estuary (Table 1).

Life-cycle categories

The fishes collected throughout the Blackwood River Estuary, including Deadwater Lagoon, comprised 29 marine species, of which 17 were marine stragglers and 12 were marine estuarine-opportunists, together with 9 estuarine/marine species and 4 estuarine species (Table 2). In terms of number of individuals, the estuarine/marine and estuarine categories, i.e. species which are able to spawn in estuaries, contributed 43.1 and 39.4%, respectively. The marine estuarine-opportunists contributed 17.2% and the marine stragglers 0.3% (Table 2).

Within each region of the estuary, the marine stragglers were represented by more species in the entrance channel (13) than in either the estuary basin (10) or Deadwater Lagoon (3) (Table 2). Marine estuarine-opportunists were represented by between 9 and 11 species in each estuarine region. While each of the 4 estuarine species was found in the three estuarine regions, more estuarine/marine species were recorded in the estuary basin (8) and entrance channel (7) than in Deadwater Lagoon (5).

In terms of number of individuals, the estuarine category made the greatest contribution in both the estuary basin and Deadwater Lagoon, i.e. 46.2 and 53.7%, respectively, but represented only 13.8% of the fishes caught in the entrance channel (Table 2). Conversely, the contribution of the estuarine/marine category in the entrance channel, i.e. 57.3%, was far greater than in any other region. However, this latter category still made a substantial contribution to the ichthyofaunas of the estuary basin and Deadwater Lagoon, in which regions it

Table 1 Life cycle categories (*E* estuarine; *E*/*M* estuarine/marine; *O* opportunist; *S* marine straggler; *SM* solely marine), minimum and maximum lengths, numbers (*N*), percentage contributions (%) and rankings by abundance (*R*) of species of elasmobranchs and teleosts caught in shallows of estuary basin, entrance channel and Deadwater Lagoon of Blackwood River Estuary and Flinders Bay between February and December 1994 (listed in order of decreasing abundance). Number of individuals of each species represents total catch of that species after numbers in each sample had been corrected to constant area of 100 m^2 (*L* length range; – species absent)

Species	Life cycle category	L (mm)	Estuary basin			Entrance channel			Deadwater Lagoon			Flinders Bay		
			N	(%)	*R*	*N*	(%)	*R*	*N*	(%)	*R*	*N*	(%)	*R*
Leptatherina wallacei	E	18–82	3537	(35.3)	1	1348	(8.1)	4	6051	(24.2)	3			
Favonigobius lateralis	E/M	12–74	2127	(21.2)	2	2894	(17.4)	3	2910	(11.6)	4			
Leptatherina presbyteroides	E/M	17–89	1359	(13.6)	3	6625	(39.8)	1	6287	(25.1)	2	2363	(76.0)	1
Pelates sexlineatus	O	9–213	1158	(11.5)	4	3546	(21.3)	2	137	(0.5)	9			
Afurcagobius suppositus	E	16–90	563	(5.6)	5	162	(1.0)	9	45	(0.2)	11			
Rhabdosargus sarba	O	10–264	378	(3.8)	6	814	(4.9)	5	1259	(5.0)	5	3	(0.1)	17
Atherinosoma elongata	E	22–101	291	(2.9)	7	570	(3.4)	6	7022	(28.1)	1			
Pseudogobius olorum	E	15–65	240	(2.4)	8	218	(1.3)	8	309	(1.2)	7			
Aldrichetta forsteri	O	21–368	202	(2.0)	9	279	(1.7)	7	447	(1.8)	6	31	(1.0)	8
Engraulis australis	E/M	42–105	36	(0.4)	10	2	(< 0.1)	26						
Sillago schomburgkii	O	34–357	22	(0.2)	11	7	(< 0.1)	19	43	(0.2)	12	48	(1.5)	7
Pseudorhombus jenynsii	O	19–245	15	(0.2)	12	19	(0.1)	12	7	(< 0.1)	15	6	(0.2)	14
Amoya bifrenatus	E/M	22–128	15	(0.2)	12	3	(< 0.1)	24	9	(< 0.1)	14			
Haletta semifasciata	S	49–154	13	(0.1)	14	9	(0.1)	15						
Enoplosus armatus	S	28–87	12	(0.1)	15	8	(< 0.1)	18						
Sillaginodes punctata	O	40–253	9	(0.1)	16	18	(0.1)	13	293	(1.2)	8			
Spratelloides robustus	S	28–110	8	(0.1)	17	25	(0.2)	11	6	(< 0.1)	16	70	(2.3)	6
Mugil cephalus	O	18–164	7	(0.1)	18	5	(< 0.1)	20	136	(0.5)	10	2	(0.1)	18
Torquigener pleurogramma	O	40–141	7	(0.1)	18	9	(0.1)	15	40	(0.2)	13	12	(0.4)	10
Scobinichthys granulatus	S	26–52	6	(0.1)	20	1	(< 0.1)	29				1	(< 0.1)	24
Pseudolabrus parilus	S	41–117	5	(0.1)	21	4	(< 0.1)	22	1	(< 0.1)	20			
Cnidoglanis macrocephalus	E/M	40–462	4	(< 0.1)	22	10	(0.1)	14	6	(< 0.1)	16	131	(4.2)	3
Penicipelta vittiger	S	54–62	4	(< 0.1)	22									
Urocampus carinirostris	E/M	57–193	3	(< 0.1)	24				6	(< 0.1)	16	2	(0.1)	18
Hyporhamphus melanochir	E/M	67–152	3	(< 0.1)	24							5	(0.2)	15
Platycephalus speculator	E/M	34–305	2	(< 0.1)	26	3	(< 0.1)	24				10	(0.3)	11
Cristiceps australis	S	46–105	1	(< 0.1)	27	5	(< 0.1)	20				2	(0.1)	18
Sillago bassensis	S	22–197	1	(< 0.1)	27	48	(0.3)	10				144	(4.6)	2
Sillago burrus	O	24	1	(< 0.1)	27									
Halichoeres brownfieldii	S	21	1	(< 0.1)	27									
Platycephalus laevigatus	S	96	1	(< 0.1)	27									
Arripis georgianus	O	42–284				4	(< 0.1)	22	4	(< 0.1)	19	9	(0.3)	12
Arripis truttaceus	O	172							1	(< 0.1)	20			
Contusus brevicaudatus	O	81–147				9	(0.1)	15	1	(< 0.1)	20	2	(0.1)	18
Stigmatophora argus	S	101–146							1	(< 0.1)	20	2	(0.1)	18
Upeneichthys sp.	S	32–36				2	(< 0.1)	26						
Pseudocaranx dentex	S	38–80				2	(< 0.1)	26						
Ammotretis elongata	S	62–146				1	(< 0.1)	29				9	(0.3)	12
Apogon rueppellii	E/M	19				1	(< 0.1)	29						
Pagrus auratus	S	147				1	(< 0.1)	29						
Kyphosus sydneyanus	S	309				1	(< 0.1)	29						
Trachurus mccullochi	S	210				1	(< 0.1)	29						
Pelsartia humeralis	SM	38–167										130	(4.2)	4
Lesueurina platycephala	SM	17–82										101	(3.2)	5
Paraplagusia unicolor	SM	25–110										19	(0.6)	9
Atherinomorus ogilbyi	O	73–162										4	(0.1)	16
Trygonorhina fasciata	SM	450–500										2	(0.1)	18
Gonorynchus greyi	O	92										1	(< 0.1)	24
Scorpis georgianus	SM	328										1	(< 0.1)	24
Total no. of species			31			34			23			26		
Total no. of fishes			10 031			16 654			25 021			3 110		

represented 35.4 and 36.8% of the total number of fishes, respectively. The contribution made by marine estuarine-opportunists in the entrance channel, i.e. 28.3%, was also relatively greater than in the estuary basin, and even more particularly Deadwater Lagoon, where they represented only 9.5% of the total fishes collected. The overall contribution of individuals to the marine straggler category was minimal, comprising <1% of the total number of fishes in the estuary basin, entrance channel and Deadwater Lagoon.

Table 2 Numbers and percentage contributions of species and individuals of each life-cycle category caught in estuary basin, entrance channel and Deadwater Lagoon regions of Blackwood River Estuary and in Flinders Bay between February and December 1994. Number of individuals of each life-cycle category represents total catch of that group after numbers in each sample had been corrected to constant area of 100 m^2

Life-cycle category	Whole estuary		Estuary basin		Entrance channel		Deadwater Lagoon		Flinders Bay	
	N	(%)	*N*	(%)	*N*	(%)	*N*	(%)	*N*	(%)
Species										
Solely marine	0	(0)	0	(0)	0	(0)	0	(0)	5	(19.2)
Marine straggler	17	(40.5)	10	(32.3)	13	(38.2)	3	(13.1)	6	(23.1)
Marine estuarine–opportunist	12	(28.6)	9	(29.0)	10	(29.4)	11	(47.8)	10	(38.5)
Estuarine/marine	9	(21.4)	8	(25.8)	7	(20.6)	5	(21.7)	5	(19.2)
Estuarine	4	(9.5)	4	(12.9)	4	(11.8)	4	(17.4)	0	(0)
Total	42		31		34		23		26	
Individuals										
Solely marine	0	(0)	0	(0)	0	(0)	0	(0)	253	(8.1)
Marine straggler	168	(0.3)	52	(0.5)	108	(0.6)	8	(<0.1)	228	(7.3)
Marine estuarine–opportunist	8876	(17.2)	1798	(17.9)	4709	(28.3)	2368	(9.5)	118	(3.8)
Estuarine/marine	22306	(43.1)	3550	(35.4)	9539	(57.3)	9218	(36.8)	2511	(80.8)
Estuarine	20356	(39.4)	4631	(46.2)	2298	(13.8)	13427	(53.7)	0	(0)
Total	51706		10031		16654		25021		3110	

Of the 26 species collected from Flinders Bay, 21 were marine species which do not spawn in estuaries (Table 2). Of these marine species, 5 have never been recorded in estuaries, and 6 are only found irregularly and in low numbers in estuaries, whereas the other 10 species also use estuaries as nursery areas, and thus belong to the marine estuarine-opportunist category. Five of the species found in Flinders Bay can spawn in both estuarine and marine waters. In terms of the number of fishes collected in Flinders Bay, the estuarine/marine category was by far the most abundant group, representing 80.8% of the overall catch, with the marine estuarine-opportunists representing only 3.8% (Table 2).

Number of species and densities in different regions

ANOVA revealed that the number of fish species differed significantly amongst the three estuarine regions and Flinders Bay, and also among months and between day and night (Table 3). However, the mean squares were far greater for region than for month and time of day. Scheffé's a posteriori test showed that the number of species was significantly greater in each of the three estuarine regions than in Flinders Bay. This point is illustrated by the fact that the mean number of species recorded monthly during both day and night was usually >5 in each of the three estuarine regions, but <5 in Flinders Bay (Fig. 3). The number of species recorded in each region was generally greater at night than during the day (Fig. 3), reflecting the fact that some of the less-abundant species tend to move near the shore at night, a feature that was also recorded for certain species in the Moore River Estuary further north in Western Australia (Young et al. 1997).

The densities of fishes also differed significantly among regions and months, but not between time of day (Table 3). The significance level and mean squares were

Table 3 Mean squares and significance levels for ANOVAs of number of species and densities of all fishes and of five most abundant species recorded in Blackwood River Estuary and Flinders Bay between February and December 1994 (*$p<0.05$, **$p<0.01$, ***$p<0.001$). Since last four species were not caught, or were caught only in very low numbers in Flinders Bay, data for these species in this region were not included in ANOVA; degrees of freedom of ANOVA for latter are given in parentheses

	Main effects, *df*			Two-way interactions, *df*			Three-way interaction, *df*	residual *df*
	Region (R), 3 (2)	Month (M), 7 (7)	Diel (D), 1 (1)	R × M, 21 (14)	R × D, 3 (2)	M × D, 7 (7)	R × M × D, 21 (14)	120 (93)
No. of species	135.13***	17.54**	47.87**	4.29	3.11	15.76	4.63	6.29
Density of fishes	13.72***	0.52*	0.14	0.23	0.38	0.21	0.31	0.22
Leptatherina presbyteroides	6.34***	1.50*	2.52*	1.17*	0.54	0.47	1.09*	0.64
Favonigobius lateralis	0.24	0.60	0.43	0.85***	0.01	0.24	0.36	0.29
Atherinosoma elongata	20.77***	4.27***	0.86	1.50***	0.53	0.26	0.40	0.28
Leptatherina wallacei	3.48***	2.23***	4.12**	2.10***	0.30	1.01	0.56	0.49
Rhabdosargus sarba	2.07**	1.12***	0.76	0.73**	0.28	0.58	0.31	0.30

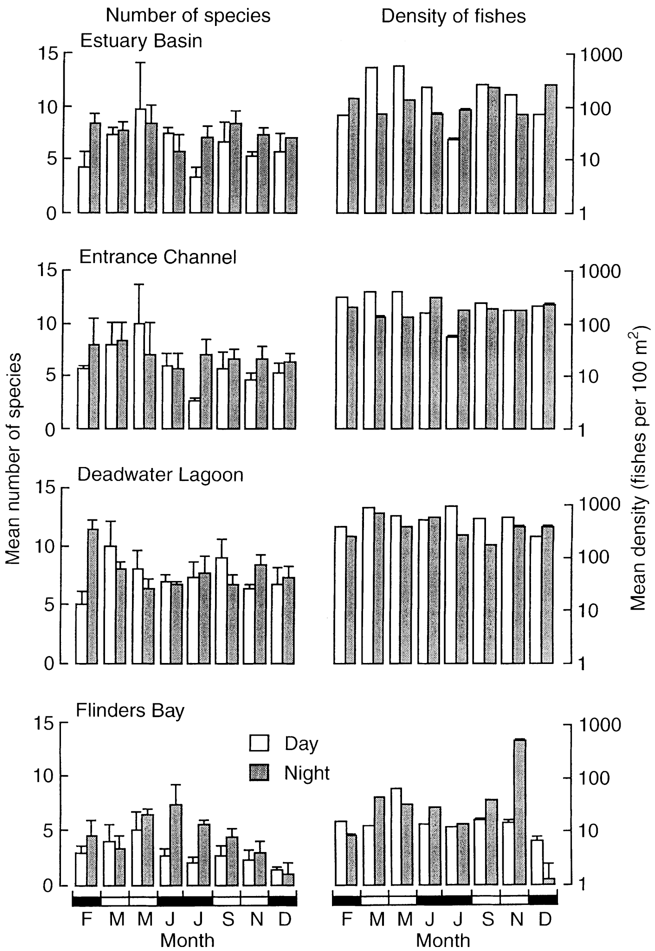

Fig. 3 Mean number of species and mean density of fishes + 1 SE in estuary basin, entrance channel and Deadwater Lagoon regions of Blackwood River Estuary and in Flinders Bay during day and night between February and December 1994 (*x*-axis as in Fig. 2)

both far higher for region than for month. Scheffé's a posteriori test showed that densities were significantly greater in each of the three estuarine regions than in Flinders Bay, and were also significantly greater in Deadwater Lagoon than in either the estuary basin or entrance channel. These differences are emphasised by the fact that the mean monthly densities of fishes during both day and night were generally <240 fishes 100 m^{-2} in Deadwater Lagoon, 120 fishes 100 m^{-2} in the entrance channel, and 68 fishes 100 m^{-2} in the estuary basin, whereas they were always <65 fishes 100 m^{-2} in Flinders Bay, except at night in November (Fig. 3).

In the case of the ANOVAs for the densities of the five most abundant species, it should be noted that *Leptatherina presbyteroides* was the only one of these species that was caught regularly and in sufficient numbers in Flinders Bay for its densities in those waters to merit inclusion in the respective ANOVAs. The densities of *L. presbyteroides*, *Atherinosoma elongata*, *L. wallacei* and *Rhabdosargus sarba* differed significantly among regions and months (Table 3). A significant diel effect was also detected in the case of *L. presbyteroides* and *L. wallacei.* There was a highly significant region × month interaction for each of the above five species, except *L. presbyteroides* (Table 3).

The mean squares for the densities of *Leptatherina presbyteroides* and *Atherinosoma elongata* were far greater for region than for month or time of day, which in turn, were higher than those for the interaction between region and month (Table 3). The results of the Scheffé's a posteriori tests for the densities of fishes in different regions were clearly reflected by the trends shown by the total numbers of individuals (Table 1). The densities of *L. presbyteroides* were significantly greater in the entrance channel and Deadwater Lagoon than in the estuary basin and Flinders Bay, and those of *A. elongata* were significantly greater in Deadwater Lagoon than in the estuary basin and entrance channel. The densities of *A. elongata* were significantly higher in September and December than in February and March. The mean squares for the densities of *L. wallacei* were similar in the case of region and time of day, both of these being slightly higher than those for month and the interaction between region and month. The densities of *L. wallacei* were significantly higher in the estuary basin than in the entrance channel, and were generally greater during the day than night. With *Rhabdosargus sarba*, the mean square for region was greater than for both month and the region × month interaction, although the significance level for month was higher than that for region and the interaction term (Table 3). The densities of *R. sarba* in Deadwater Lagoon were significantly greater than those in the estuary basin or entrance channel.

The significant interaction between region and month for each species often partly reflected the fact that the increase in freshwater discharge and/or decline in salinity that occurs in the estuary basin and entrance channel in winter had an influence on the densities of these species in these regions, whereas this was not the case in Deadwater Lagoon, where these environmental parameters exhibited far less variability.

Classification and ordination

Classification of the mean densities of each species during day and night in each region and in each month separated the samples collected from the three regions inside the estuary (Group A) from those obtained from Flinders Bay (Group B) (Fig. 4). Samples from the estuarine regions then separated into two major groups, one containing mainly samples from the estuary basin and entrance channel during late summer and autumn (Group C), and the other comprising those taken from the same two regions during winter, spring and early summer, together with the majority of those from Deadwater Lagoon throughout the year (Group D). The latter group then separated into one group (E) that comprised samples from the estuary basin and entrance channel and another group (F) that consisted mostly of samples from Deadwater Lagoon (Fig. 4).

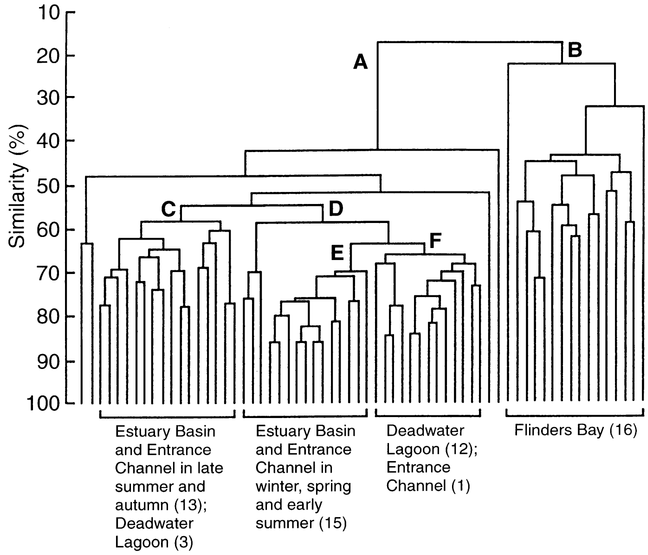

Fig. 4 Classification (Groups A to F) of mean densities recorded for each fish species in estuary basin, entrance channel and Deadwater Lagoon regions of Blackwood River Estuary and in Flinders Bay during day and night between February and December 1994. No. of samples for each region is given in parentheses

The results of the non-metric multidimensional-scaling ordination paralleled those produced by classification. Thus, samples from the three estuarine regions formed a group that was totally distinct from those collected from Flinders Bay (Fig. 5a). The samples for both day and night within the latter group were far more widely dispersed than those collected during the day and night in any of the three estuarine regions (Table 4, Fig. 5a). Ordination of samples from the three estuarine regions, independent of those from Flinders Bay, resulted in samples from the estuary basin and entrance channel during late summer and autumn forming a group to the left of those taken from these regions during winter, spring and early summer (Fig. 5b). Furthermore, these two groups were separate from those constituting samples taken in Deadwater Lagoon throughout the year (Fig. 5b).

SIMPER revealed that the species composition of Flinders Bay was characterised by *Lesueurina platycephala*, whereas that of the estuary was characterised by *Favonigobius lateralis*, *Leptatherina wallacei* and *Rhabdosargus sarba*. ANOSIM demonstrated that, within the estuary, the compositions of the fish fauna in Deadwater Lagoon during both day and night differed

Table 4 Relative dispersion values for ordination plots for samples collected during day and night in estuary basin, entrance channel and Deadwater Lagoon regions of Blackwood River Estuary and in Flinders Bay between February and December 1994

	Estuary basin	Entrance channel	Deadwater Lagoon	Flinders Bay
Day	0.79	1.02	0.91	1.45
Night	0.79	0.75	0.62	1.67

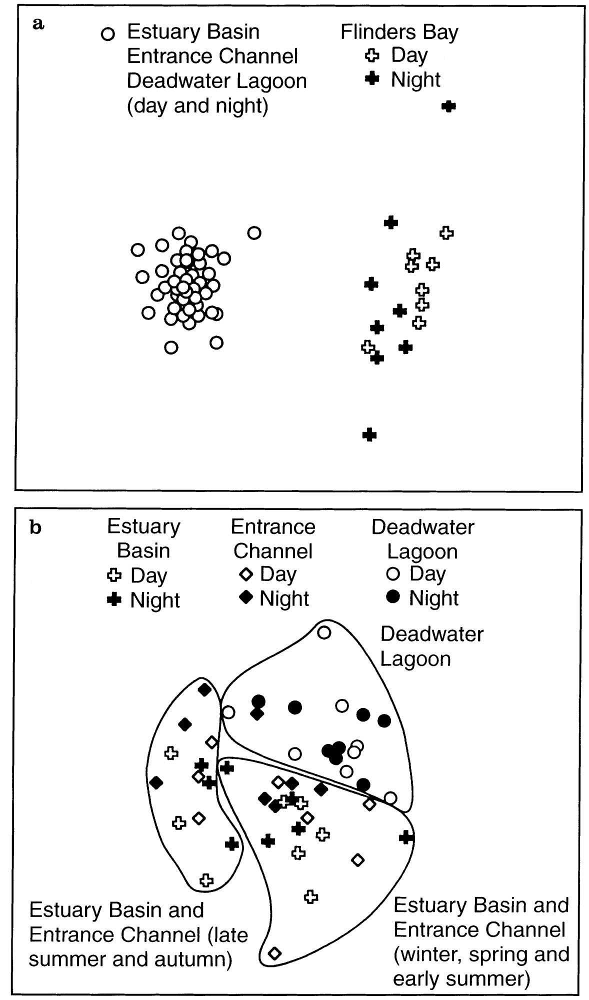

Fig. 5 Ordination of mean densities recorded for each fish species in Blackwood River Estuary during day and night and in Flinders Bay between February and December 1994 (**a**) and in estuary basin, entrance channel and Deadwater Lagoon regions of Blackwood River Estuary during day and night between February and December 1994 (**b**) (Note: lines enclose samples of each of the three designated groups; each contains all the samples in that group)

significantly from those during both day and night in the estuary basin and entrance channel. *Atherinosoma elongata* typified Deadwater Lagoon, while *Afurcagobius suppositus* typified the estuary basin and entrance channel.

Comparisons between marine estuarine-opportunists in *Ruppia megacarpa* and bare sand

A total of 7 156 fishes and 17 species and 7 390 fishes and 10 species were caught in *Ruppia megacarpa* and over bare sand, respectively, on the four separate occasions when these extreme habitat types were sampled between May 1994 and January 1995. The mean number of species in these four months ranged from 7.0 to 8.0 in *R. megacarpa* and from 5.2 to 6.0 over bare sand. Three marine species, *Rhabdosargus sarba*, *Pelates sexlineatus* and *Aldrichetta forsteri*, were represented in the samples obtained collectively from dense *R. megacarpa* and over bare sand by 866, 221 and 103 individuals, respectively. The mean densities of *Rhabdosargus sarba* were greater in *Ruppia megacarpa* than over bare sand in each month, and *Pelates sexlineatus* was only ever caught in *R. megacarpa.* In contrast, 66% of the *A. forsteri* were caught over bare sand.

Discussion

Comparison between ichthyofaunas of Blackwood River Estuary and Flinders Bay

Classification and ordination demonstrated that the ichthyofaunal composition of the shallows of Flinders Bay, immediately outside the mouth of the Blackwood River Estuary, differs markedly from that of the shallows within the estuary, including that of Deadwater Lagoon. This difference is largely attributable to the fact that the samples collected from Flinders Bay yielded five marine species that were not found in the Blackwood River Estuary (and have also not been recorded in other south-western Australian estuaries), and did not yield any of the four strictly estuarine species which were caught in that estuary. The differences are further compounded by the fact that only two of the most abundant species in each of the three regions of the estuary, i.e. *Leptatherina presbyteroides* and *Aldrichetta forsteri*, ranked amongst the most abundant species in that embayment.

Although *Leptatherina presbyteroides* was very abundant at times in Flinders Bay, all other species that spawn in both marine and estuarine waters, and were caught in the Blackwood River Estuary, were either absent or present in very low densities in Flinders Bay, except for *Cnidoglanis macrocephalus.* However, this last species, which was represented only by juveniles in Flinders Bay, was predominantly caught on those occasions when detached macrophytes were present. Detached macrophytes have been shown to provide an important nursery habitat for this and other species elsewhere in marine waters in south-western Australia (Lenanton et al. 1982; Lenanton and Caputi 1989). Although the sampling sites in Flinders Bay were moderately protected and typical of many such marine areas in south-western Australia, they were not as protected as those extreme cases where the shore line is particularly well-sheltered by prominent headlands and/or offshore reefs (Ayvazian and Hyndes 1995; Hyndes et al. 1996). This would account for the presence in Flinders Bay of species such as *Sillago bassensis*, as the juveniles of this species do not require highly protected waters as a nursery area (Hyndes et al. 1996), and for the absence of *Favonigobius lateralis* from this bay, as this species tends to occur only in very sheltered regions (Gill and Potter 1993). The far higher dispersion values for the ichthyofauna of Flinders Bay than for those of any of the three estuarine regions presumably reflects the greater fluctuations that occur in this environment through variations in the degree of wave activity and the relative volume of detached macrophytes.

Despite the fact that marine species such as *Pelates sexlineatus*, *Rhabdosargus sarba*, *Aldrichetta forsteri*, *Mugil cephalus* and *Sillaginodes punctata* were very abundant in the estuary, they were either never found or were far less common in Flinders Bay. Since these teleosts were largely represented by their juveniles, the estuary is apparently a "preferred" nursery habitat for these species, which are also very abundant in estuaries elsewhere in southern Australia (Potter et al. 1983, 1993; Loneragan et al. 1989; Connolly 1994; Potter and Hyndes 1994; Jones et al. 1996; West and King 1996). In contrast, the juveniles of *Sillago schomburgkii* were moderately abundant in both environments and those of *Spratelloides robustus* and *Sillago bassensis* were relatively far more abundant in Flinders Bay than in the estuary, as is also the case in other estuaries and nearby marine embayments in south-western Australia (Potter et al. 1983; Loneragan et al. 1989; Ayvazian and Hyndes 1995; Hyndes et al. 1996). However, certain marine species, e.g. *Pelsartia humeralis* and *Lesueurina platycephala*, that were abundant in Flinders Bay and are also numerous in other nearshore marine waters of south-western Australia (Lenanton 1982; Ayvazian and Hyndes 1995), were not found in the Blackwood River Estuary and have not been recorded in other estuaries in the region. Thus, the marine species found in nearshore waters form a spectrum regarding their "preferred" nursery areas, with those at one end showing a marked tendency to use estuaries for this purpose, while those at the other end utilise only marine waters.

The far higher overall density of fishes in the Blackwood River Estuary than in Flinders Bay suggests that this estuary provides a greater source of food and/or protection than is offered by nearby moderately-protected and nearshore marine waters, although such differences between these two habitat types are probably typical of the situation along the coastline of southern Australia.

Ichthyofaunal composition of basin and entrance channel of Blackwood River Estuary

The large numbers of the juveniles of marine estuarine-opportunists such as *Pelates sexlineatus*, *Rhabdosargus sarba*, *Aldrichetta forsteri* and *Sillaginodes punctata* that entered the shallows of the Blackwood River Estuary in 1994 parallels the situation recorded 20 yr earlier in this estuary (Lenanton 1977) and that found more recently in other large estuaries northwards on the lower west coast of Australia, such as the Swan and Peel–Harvey estuaries (Loneragan et al. 1986; Loneragan and Potter 1990). However, the fish faunas in both the estuary basin and entrance channel of the Blackwood River Estuary were dominated by the small teleosts *Leptatherina wallacei*, *Favonigobius lateralis* and *L. presbyteroides*, which are each able to complete their life cycles in estuarine waters and, in the case of the latter two species, also protected marine waters (Prince et al. 1982; Prince and Potter 1983; Potter et al. 1990; Neira et al. 1992). These three species, and other estuarine-spawning atherinids and gobiids, are also amongst the most abundant teleosts in the shallow waters of estuaries elsewhere in temperate Australia (Loneragan et al. 1986; Potter et al. 1993; Connolly 1994; Molsher et al. 1994; Pollard 1994; Potter and Hyndes 1994) and in southern Africa (Bennett 1989; Potter et al. 1990). The overwhelming contribution made by estuarine-spawning species to these ichthyofaunas contrasts with the situation in temperate estuaries of the northern hemisphere, where such fish faunas are dominated by the juveniles of marine species (Dando 1984; Yoklavich et al. 1991; Potter et al. 1997). The large contribution made to the ichthyofaunas of temperate Australian estuaries by estuarine-spawning species probably reflects, in part, the consequences of the landlocking to which these estuaries, including that of the Blackwood River, have been subjected at some time through the closure of their narrow estuary mouths (Potter et al. 1990). Such landlocking still occurs, either seasonally or for longer periods, in several estuaries along the south coast of Western Australia (Lenanton and Hodgkin 1985).

Influence of freshwater discharge and/or salinity declines

Classification and ordination emphasised that the ichthyofaunas of the estuary basin and entrance channel both underwent pronounced changes in winter. This change occurred when the heavy and highly seasonal rainfall that characterises south-western Australia resulted in a massive increase in freshwater discharge and a consequent marked decline in salinities to ~2‰ in the estuary basin and 4‰ in the entrance channel. The change in the ichthyofaunas of these regions was attributable, in part, to a pronounced decline in the numbers of marine straggler species and of marine estuarine-opportunist species, particularly of *Pelates sexlineatus* and *Rhabdosargus sarba*. The tendency for certain marine species to leave the estuary at times when freshwater discharge increases markedly and the salinity declines to very low levels parallels the situation in morphologically similar estuaries in southern Africa (Bennett 1989; Whitfield and Kok 1992). The conclusion that this emigration of marine species was related specifically to changes in freshwater discharge and/or salinity, rather than to just a seasonal migration, is substantiated by the fact that such an emigration did not occur in Deadwater Lagoon in which, through the absence of tributary rivers, the salinities remained at levels >28‰ in all but one month and, even in that month, only declined to 23‰. It was particularly noteworthy that, in contrast to the situation in the estuary basin and entrance channel, large numbers of *R. sarba* remained in Deadwater Lagoon throughout the winter and spring. The faunal change in the estuary basin in winter also reflects the immigration from the sea of new 0+ recruits of *Aldrichetta forsteri*, a species which, in south-western Australia, enters estuaries between late autumn and late spring, when freshwater discharge ensures that estuary mouths are open (Chubb et al. 1981). The faunal change was also enhanced by the immigration from riverine areas of *Leptatherina wallacei*, a species which, in estuaries, is often most abundant in regions of low salinity but is subject to the effects of freshwater flushing (Prince et al. 1982; Loneragan and Potter 1990). However, *L. wallacei* did occur in areas of high salinity in Deadwater Lagoon where dense beds of *Ruppia megacarpa* are present, as is also the case in Wilson Inlet (Humphries and Potter 1993).

Colonisation of Deadwater Lagoon and influence of *Ruppia megacarpa*

The far greater overall density of fishes in Deadwater Lagoon than in either the entrance channel or even the estuary basin is presumably related, at least in part, to the higher productivity and greater protection from predators that must result from the presence of the extensive patches of *Ruppia megacarpa* that are found throughout this lagoonal water body. Despite the increase in structural heterogeneity that is produced by the patches of *R. megacarpa* in Deadwater Lagoon, the total number of species in that water body was lower than in the estuary basin. This largely reflected the immigration of a far lower number of marine straggler species into Deadwater Lagoon than into the estuary basin, presumably because the tidal flow through its narrow and shallow side channel from the entrance channel is far weaker than that of the more direct flow which occurs through the entrance channel into the estuary basin. However, the fact that the marine estuarine-opportunists *Rhabdosargus sarba*, *Aldrichetta forsteri*, *Sillaginodes punctata* and *Mugil cephalus* each attained far higher densities in Deadwater Lagoon than in the estuary basin emphasises that, although the chances of colonisation of the former region by marine species is less likely, once the members of a species have migrated into that water body, they remain there and capitalise on its productive and protected environment. It should also be recognised that the overall abundance of *Atherinosoma elongata* and *Leptatherina wallacei*, which prefer *Ruppia megacarpa* to bare sand (Humphries and Potter 1993), were greater in Deadwater Lagoon than in the estuary basin or entrance channel.

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References

Ayvazian SG, Hyndes GA (1995) Surf-zone assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? Mar Biol 122: 527–536

Bell JD, Pollard DA (1989) Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Oxford, pp 565–609

Bennett BA (1989) A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the south-western Cape, South Africa. S Afr J mar Sci 8: 43–55

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17: 143–162

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. Estuar, cstl Shelf Sci 40: 177–193

Chubb CF, Potter IC, Grant CJ, Lenanton RCJ, Wallace J (1981) The age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan–Avon River system, Western Australia. Aust J mar Freshwat Res 32: 605–628

Claridge PN, Potter IC, Hardisty MW (1986) Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn Estuary. J mar biol Ass UK 66: 229–258

Clark BM, Bennett BA, Lamberth SJ (1994) A comparison of the ichthyofauna of two estuaries and their adjacent surf zones with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. S Afr J mar Sci 14: 121–131

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18: 117–143

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth

Connolly RM (1994) A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. Aust J mar Freshwat Res 45: 1033–1044

Cronin E, Mansueti AJ (1971) The biology of the estuary. In: Douglas PA, Stroud RH (eds) A symposium on the biological significance of estuaries. Sport Fishing Institute, Washington D.C., pp 16–39

Dando PR (1984) Reproduction in estuarine fish. In: Potts GW, Wootton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, London, pp 155–170

Day JH (1981) The nature, origin and classification of estuaries. In: Day JH (ed.) Estuarine ecology with particular reference to southern Africa. Balkema, Rotterdam, pp 1–6

Gill HS, Potter IC (1993) Spatial segregation amongst goby species within an Australian estuary, with a comparison of the diets and salinity tolerance of the two most abundant species. Mar Biol 117: 515–526

Haedrich RL (1983) Estuarine fishes. In: Ketchum BH (ed) Ecosystems of the world. 26. Estuaries and enclosed seas. Elsevier, Amsterdam, pp 183–207

Hodgkin EP (1978) An environmental study of the Blackwood River Estuary, Western Australia, 1974–1975. Government Printer, Perth

Hodgkin EP, Lenanton RC (1981) Estuaries and coastal lagoons of south Western Australia. In: Nielson BJ, Cronin LE (eds) Estuaries and nutrients. Humana Press, New Jersey, pp 309–321

Humphries P, Potter IC (1993) Relationship between the habitat and diet of three species of atherinids and three species of gobies in a temperate Australian estuary. Mar Biol 116: 193–204

Humphries P, Potter IC, Loneragan NR (1992) The fish community in the shallows of a temperate Australian estuary: relationships with the aquatic macrophyte *Ruppia megacarpa* and environmental variables. Estuar, cstl Shelf Sci 34: 325–346

Hyndes GA, Potter IC, Lenanton RCJ (1996) Habitat partitioning by whiting species (Sillaginidae) in coastal waters. Envir Biol Fish 45: 21–40

Jones GK, Baker JL, Edyvane K, Wright GJ (1996) Nearshore fish community of the Port River–Barker Inlet Estuary, South Australia. I. Effect of thermal effluent on the fish community structure, and distribution and growth of economically important fish species. Aust J mar Freshwat Res 47: 785–799

Kennish MJ (1990) Ecology of estuaries. Volume II. Biological aspects. CRC Press, Boca Raton, Florida

Kikuchi T (1980) Faunal relationships in temperate seagrass beds. In: Phillips RC, McRoy CP (eds) Handbook of seagrass biology: an ecosystem perspective. Garland, New York, pp 153–172

Lenanton RCJ (1977) Aspects of the ecology of fish and commercial crustaceans of the Blackwood River Estuary, Western Australia. Fish Bull West Aust 19: 1–72

Lenanton RCJ (1982) Alternative non-estuarine nursery habitats for some commercially and recreationally important fish of south-western Australia. Aust J mar Freshwat Res 33: 881–900

Lenanton RCJ, Caputi N (1989) The roles of food supply and shelter in the relationship between fishes, in particular *Cnidoglanis macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. J exp mar Biol Ecol 128: 165–176

Lenanton RCJ, Hodgkin EP (1985) Life history strategies of fish in some temperate Australian estuaries. In: Yanez-Arancibia A (ed) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. UNAM Press, Mexico, pp 267–283

Lenanton RCJ, Potter IC (1987) Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. Estuaries 10: 28–35

Lenanton RCJ, Robertson AI, Hansen JA (1982) Nearshore accumulations of detached macrophytes as nursery areas for fish. Mar Ecol Prog Ser 9: 51–57

Loneragan NR, Potter IC (1990) Factors influencing community structure and distribution of different life-cycle categories of fishes in shallow waters of a large Australian estuary. Mar Biol 106: 25–37

Loneragan NR, Potter IC, Lenanton RCJ (1989) Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. Mar Biol 103: 461–479

Loneragan NR, Potter IC, Lenanton RCJ, Caputi N (1986) Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. Mar Biol 92: 575–586

Molsher RL, Geddes MC, Paton DC (1994) Population and reproductive ecology of the small-mouthed hardyhead *Atherinosoma microstoma* (Günther) (Pisces: Atherinidae) along a salinity gradient in the Coorong, South Australia. Trans R Soc S Aust 118: 207–216

Neira FJ, Potter IC, Bradley JS (1992) Seasonal and spatial changes in the larval fish fauna within a large temperate Western Australian estuary. Mar Biol 112: 1–16

Pollard DA (1994) A comparison of fish assemblages and fisheries in intermittently open and permanently open coastal lagoons on the south coast of New South Wales, south-eastern Australia. Estuaries 17: 631–646

Potter IC, Beckley LE, Whitfield AK, Lenanton RCJ (1990) Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and southern Africa. Envir Biol Fish 28: 143–178

Potter IC, Claridge PN, Hyndes GA, Clarke KR (1997) Seasonal, annual and regional variations in the composition of the ichthyofauna in the Inner Severn Estuary and Inner Bristol Channel. J mar biol Ass UK (in press)

Potter IC, Hyndes GA (1994) The composition of the fish fauna of a permanently open estuary on the southern coast of Australia, and comparisons with a nearby seasonally closed estuary. Mar Biol 121: 199–209

Potter IC, Hyndes GA, Baronie FM (1993) The fish fauna of a seasonally closed Australian estuary. Is the prevalence of estuarine-spawning high? Mar Biol 116: 19–30

Potter IC, Loneragan NR, Lenanton RCJ, Chrystal PJ, Grant CJ (1983) Abundance, distribution and age structure of fish populations in a Western Australian estuary. J Zool Lond 200: 21–50

Prince JD, Potter IC (1983) Life-cycle duration, growth and spawning times of five species of Atherinidae (Teleostei) found in a Western Australian estuary. Aust J mar Freshwat Res 34: 287–301

Prince JD, Potter IC, Lenanton RCJ, Loneragan NR (1982) Segregation and feeding of atherinid species (Teleostei) in southwestern Australian estuaries. Aust J mar Freshwat Res 33: 865–880

Somerfield PJ, Clarke KR (1997) A comparison of some methods commonly used for the collection of sublittoral sediments and their associated fauna. Mar envirl Res 43: 145–156

West RJ, King RJ (1996) Marine, brackish, and freshwater fish communities in the vegetated and bare shallows of an Australian coastal river. Estuaries 19: 31–41

Whitfield AK, Kok HM (1992) Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. JLB Smith Institute of Ichthyology, Grahamston, South Africa

Yoklavich MM, Cailliet GM, Barry JP, Ambrose DA, Antrim BS (1991) Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. Estuaries 14: 465–480

Young GC, Potter IC, Hyndes GA, de Lestang S (1997) The ichthyofauna of an intermittently open estuary. Implications of bar breaching and low salinities on faunal composition. Estuar, cstl Shelf Sci (in press)