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Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary *

F. J. Neira, I. C. Potter and J. S. Bradley

School of Environmental and Life Sciences, Murdoch University, Murdoch, Western Australia 6150, Australia

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Abstract. A total of 66 814 fish larvae, representing 37 families and 74 species, were collected in samples taken monthly between January 1986 and April 1987 from 13 sites located at frequent intervals throughout the large Swan Estuary in south-western Australia. The Gobiidae was the most abundant family, comprising 88.2% of the total number of larvae, followed by the Clupeidae (3.4%), Engraulididae (2.9%) and Blenniidae (1.0%). The most abundant species were *Pseudogobius olorum* (53.3%), *Arenigobius bifrenatus* (31.2%) and *Engraulis australis* (2.9%). Abundance of fish larvae in the lower, middle and upper regions of the estuary each reached a maximum between mid-spring and early summer, 2 to 4 mo before the attainment of maximum temperatures. Larvae of species such as *Nematalosa vlaminghi* and *Apogon rueppellii* were collected only between November and February, whereas those of others such as *P. olorum*, *E. australis* and *Leptatherina wallacei* were present over many months. The times and locations of capture of larvae have been related to the distribution and breeding periods of the adults of these species. The mean monthly number of species was far greater in the lower than upper estuary (14.7 vs 2.7), whereas the reverse was true for mean monthly concentration (42 vs 197 larvae per 100 m^3). Classification, using the abundance of each of the 74 species recorded at the different sites, showed that the composition of the larval fish fauna in the lower, middle and upper estuary differed markedly from each other. Most larvae caught in the lower estuary belonged to marine species, whereas those in the upper estuary almost exclusively represented species that spawn within the estuary. The fact that the larvae of the 59 species of marine teleosts recorded during this study were restricted mainly to the lower estuary, and yet contributed only 6.2% to the total numbers for the whole estuary, helps to account for the relatively high species diversity in this region. The lack of penetration of many of these larvae beyond the first 12.5 km of the estuary presumably reflects the weak tidal effect in the wide basins of the middle estuary and saline regions of the tributary rivers. The larvae of the 13 teleosts that typically spawn within the estuary contributed 93.8% to the total numbers of larvae. Most of these estuarine-spawned larvae belong to teleosts that deposit demersal eggs and/or exhibit parental care (egg-guarding and oral and pouch-brooding), characteristics which would maximize their chances of retention within the estuary.

* Please address all correspondence and requests for reprints to F. J. Neira at Murdoch University

Introduction

The fish found in estuaries are mainly marine species which enter these systems either infrequently and usually in small numbers, or regularly and in large numbers (Blaber and Blaber 1980, Haedrich 1983, Dando 1984, Claridge et al. 1986, Potter et al. 1990). These two groups have been termed marine stragglers and marine estuarine-opportunists, respectively (Lenanton and Potter 1987). Estuaries also provide the route through which anadromous and catadromous species migrate between rivers and the sea (McDowall 1988). In general, relatively few species complete their life cycles within estuaries and the distribution of freshwater teleosts only occasionally extends into estuarine waters (Cronin and Mansueti 1971, Haedrich 1983, Dando 1984).

Many of the studies on larval fishes in estuaries have concentrated on elucidating the way in which marine species are transported through these systems (e.g. Weinstein et al. 1980, Fortier and Leggett 1982, Norcross and Shaw 1984, Boehlert and Mundy 1988). Other studies have demonstrated that estuarine species typically produce demersal and adhesive eggs, a feature which would facilitate their retention within estuaries (Pearcy and Richards 1962, Able 1978, Haedrich 1983, Dando 1984). However, there have been only a few studies that have investigated the way in which the ichthyoplankton changes seasonally throughout the length of estuaries (Pearcy and Richards 1962, Pearcy and Myers 1974, Melville-Smith and Baird

1980). Moreover, no study has attempted to quantify the relative contributions of the species representing the different life cycle categories to the ichthyofauna of estuaries and their different regions.

Studies on the fish fauna of the large Swan Estuary in south-western Australia have demonstrated that this system contains a greater than usual incidence of teleost species that are capable of completing their life cycles in an estuarine environment (Loneragan et al. 1989, Potter et al. 1990). The relatively high incidence of estuarine teleost populations *sensu stricto* in the Swan and other south-western Australian estuaries might reflect adaptations to the periodic landlocking to which these estuaries have been subjected and/or the relatively stable conditions that prevail within these systems for much of the year, as a result of the small tidal action and the restriction of strong freshwater discharge to a limited period (Spencer 1956, Hodgkin and Di Lollo 1958, Potter et al. 1986, Hodgkin 1987). These species are typically far more abundant in the shallows of the basins in the middle estuary and the saline reaches of their two tributaries than in the long entrance channel, whereas the reverse is true for marine stragglers and marine estuarine-opportunists (Loneragan et al. 1989). Some estuarine species, such as *Pseudogobius olorum* and *Atherinosoma wallacei*, typically spend their juvenile and adult life in a restricted region of the estuary. Although species such as *Nematalosa vlaminghi*, *Amniataba caudavittatus*, and *Apogon rueppellii*, are more widespread and, in the case of the first species spend a period at sea, their spawning is still concentrated in particular areas within one of the main regions of the esutary (Prince and Potter 1983, Chubb and Potter 1984, Chrystal et al. 1985, Loneragan et al. 1989, H. S. Gill personal communication). It is also now evident that the spawning period of some of these species is relatively short, e.g. *Apogon rueppellii* whereas that of others is prolonged, e.g. *P. olorum* (Chrystal et al. 1985, H. S. Gill personal communication). The above localisations in space and time will influence the community structure of the larval fish fauna in the different regions of the estuary.

Despite the extensive data available on the biology of the juvenile and adult fish fauna of the Swan and other south-western Australian estuaries (see references in Potter et al. 1990), the work of Gaughan et al. (1990) on the seasonal occurrence of ichthyoplankton in the lower Swan Estuary is the sole detailed study of this kind in any estuary in Western Australia. Indeed, data on the seasonal occurrence of fish larvae in estuaries in other parts of Australia (Miskiewicz 1986, Ramm 1986, Steffe and Pease 1988) and elsewhere in the Southern Hemisphere (Whitfield 1989) is limited to that occurring in certain regions of these systems. Furthermore, relatively little substantial data are available on the larval fish faunas of inshore waters in temperate regions of the Southern Hemisphere (Beckley 1986, Jenkins 1986, Roper 1986, Miskiewicz 1987, Steffe 1989).

Since previous studies in the Swan Estuary have indicated that the spawning areas of several species are spatially and seasonally localised within this system (see third paragraph above), we have examined the hypothesis that the larvae of these species will also be restricted to certain regions and times of the year. Whenever possible we have compared the distribution of the larvae of species known to spawn in the estuary with those of their juveniles and adults and consider the results in the context of data on breeding location and period. Since the tidal action within this estuary is small, we have also examined the hypothesis that the larvae of marine species will show limited penetration of the estuary. We also describe the species composition of the larval fish fauna and the way in which the abundance of the larvae of all species and of the most abundant species, and the species richness, diversity and evenness of the larval assemblage, change spatially and seasonally throughout the system. In addition, the relative contributions made by the larvae representing each life-cycle category, both to the total number of species recorded as larvae and to the total numbers of all fish larvae, have been calculated for both the whole estuary and for each of its three main regions. Classification has been employed to elucidate the degree to which the larval fish fauna at the various sites differed and to attempt to relate any marked differences to the types of life cycles exhibited by the main species found as larvae in the different estuary regions. Since we have postulated that the larvae of many species will be localised within the estuary and within restricted periods, and as this would produce concomitant changes in the community variables, we have sampled a substantial number of sites throughout the length of the Swan Estuary at monthly intervals.

Materials and methods

Study area

The large, permanently open Swan Estuary (32°03.2'S; 115°44.0'E) comprises a long, narrow entrance channel leading into two large basins which in turn are supplied by two main tributaries, the Avon and Canning rivers (Fig. 1). The entrance channel, basins and saline reaches of the tributary riverine areas have been termed the lower, middle and upper estuary, respectively (Chalmer et al. 1976). The estuary, which covers a surface area of approx 53 km^2, extends from the entrance of Fremantle Harbour 28 km upstream to Kent Street Weir in the Canning River and 60 km upstream in the main channel of the Swan River to the point where Ellen Brook joins the Avon River (Hodgkin 1987, and present Fig. 1).

Sampling regime

Sampling for fish larvae was carried out in the middle of each month between January 1986 and April 1987 at Sites 1 and 2 in the lower estuary, Sites 3 to 7 in the middle estuary and Sites 8 to 13 in the upper estuary (Fig. 1). The most downstream site (1) and most upstream site (13) were 3.0 and 44.7 km from the estuary mouth, respectively. Although water depth ranged from 5 to 21 m at Sites 1–3, it was always <2.5 m and sometimes <1.5 m at Sites 4–13. The time and direction of each tow at each of the 13 sites was selected so that each tow would cover about 700 m of water, which means that cumulatively about one-fifth of the total length of the estuary would be sampled. The analysis of the larval catches was very labour-intensive, especially since the larvae of most of the species had not been described, but the resultant time-series data, based on this extensive sampling regime, which involved monthly

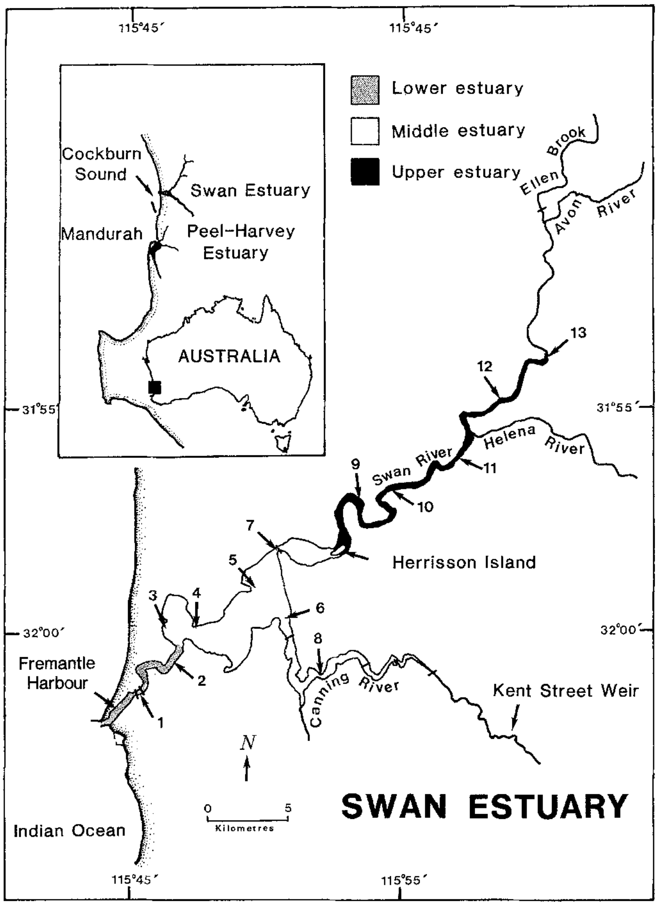

Fig. 1. Location of sampling sites (1–13) in lower, middle and upper Swan Estuary

samples at a series of sites throughout the estuary, were considered likely to provide clear indications as to where the various species were localised in space and time.

Sampling was carried out on two successive nights, commencing 1 h after sunset and finishing ~4 to 5 h later. Sampling on the first night started at Site 13 and continued downstream to Site 8, and on the second night extended from Site 7 to Site 1. Prior to sampling each site, the surface salinity and temperature were measured using a portable YEO-KAL salinity-temperature bridge. Samples were collected using two 0.5 mm mesh conical nets, 0.6 m in diameter and 2.0 m in length, which were joined together by a 200 mm-long aluminium plate. An everted cone-shaped structure, with 90 mm-aperture mesh, was placed at the mouth of each net to prevent the entry of jellyfish. The two nets were towed just below the surface for 10 min at a speed of 1.5 to 2.0 m s^{-1}. The volume of water filtered by each net during each tow (97 to 340 m^3) was measured using a General Oceanics digital flowmeter. After the completion of each tow, both nets were washed and the samples fixed in 10% buffered formalin and stored in 70% alcohol.

Fish larvae were removed from samples using a dissecting microscope and identified to the lowest possible taxon and counted. Subsampling of plankton was undertaken on the few occasions when the number of larvae in the sample from a site was estimated as exceeding ~2000. The term larva used in this paper included the yolk-sac, preflexion, flexion and postflexion stages as described by Leis and Rennis (1983). Identifications of larvae were based on the descriptions of Uchida et al. (1958), Russell (1976), Miller et al. (1979), Crossland (1981, 1982), Fahay (1983), Leis and Rennis (1983), Moser et al. (1984) and Leis and Trnski (1989) and on the series method (Leis and Rennis 1983). Larvae that could not be identified at either the species, genus or family level (including damaged specimens) were placed in the unidentified category (Table 1: Rank 16). Representatives of most of the larvae collected during the present study were placed in the Australian Museum (Sydney).

Life-cycle designations

Each species has been placed in one of the following categories: marine straggler (S), marine estuarine-opportunist (O), estuarine (E), anadromous (A) or freshwater (F) (Table 1), following the designations given to the fish species found in the Swan Estuary by Loneragan et al. (1989). Some of the species included in the estuarine category also breed in protected inshore marine waters (Chrystal et al. 1985, Potter et al. 1986, Loneragan et al. 1989). Since the Perth herring (*Nematalosa vlaminghi*) migrates from the sea to its spawning areas at the top of the estuary (Chubb and Potter 1984), it has for convenience been categorized as an anadromous species.

Six marine species collected as larvae during the current study (*Vanacampus phillipi*, *Arnoglossus* sp., *Lesueurina* sp., *Lampadena* sp., *Strabozebrias cancellatus* and *Aulopus purpurissatus*) had never been recorded as juveniles or adults during previous extensive studies of juvenile and adult fishes in the Swan Estuary (Loneragan et al. 1989). Since the larvae of these species were also rare and largely confined to the lower estuary, they were placed in the marine straggler category (Table 1).

Treatment of data

The total number of larvae and the numbers of each species caught in both nets at each site and in each month were summed and converted to a concentration, i.e., numbers per 100 m^3. Since samples were collected between January and April in 1986 as well as in 1987, the concentrations for each of these four months in the two years have been averaged to provide data for each of the twelve months of the calendar year. The values in Figs. 3 and 5 for the larval fish community represent the mean of the concentrations for the 12 mo of the year at the different sites and for the lower, middle and upper estuary over the 16 mo of the study, respectively. The numbers of fish larvae shown in Figs. 6–9 correspond to the sum of the numbers of fish larvae at the 13 sites (Figs. 6, 7) and for the 12 mo of the year (Figs. 8, 9), after the numbers in each sample had been adjusted to a volume of 100 m^3. The above data on numbers at the various sites over the 12 mo of the year were used to determine the percentage contributions of taxa to the larval fish fauna of (i) the lower, middle and upper regions of the estuary, (ii) the whole system and (iii) the different life-cycle categories.

The Shannon-Wiener (H') and Pielou's evenness (J) indices were calculated for each site using the method specified in Pielou (1975).

For the single species (*Pseudogobius olorum*), which was distributed throughout the estuary and abundant over a protracted period, a repeated-measures analysis of variance was performed on $\log_{10}(n+1)$-transformed data to ascertain whether significant differences in seasonality occurred between regions. The analysis utilised the repeated-measures facilities of the MANOVA procedure of the SPSSX statistical package (SPSSX), using the ANALYSIS (REPEATED) subcommand. Sites were defined as the subjects, regions as between-subjects factors, and months as within-subjects factors. The hypothesis of interest in this analysis was the region × month interaction and, more specifically, the overall similarity of the changes in the time-series pattern of abundance, which could be examined by polynomial regression coefficients for the different regions. Initially, a Wilks' lambda multivariate test of the interaction was applied as this is the more general of the repeated-measures tests. Since in this case the number of months exceeded the number of sites, precluding the application of this test to the full data, a restricted number of months (July 1986 to April 1987) were included, and the test proved non-significant. However, following Crowder and Hand (1990), we decided to apply the univariate F-tests which impose no restriction on the number of months included.

Table 1. Rank by abundance of families and species of fishes collected as larvae from 13 sites located throughout Swan Estuary, based on collections made between January 1986 and April 1987. Except for values for total number of larvae, the rank and all other values in this and Tables 2 and 3 have been calculated from numbers obtained for each site over the 12 mo of the year, after catches in each sample have been adjusted to a constant volume of 100 m^3 (see "Materials and methods – Treatment of data" for further details). Percentages for contributions of each family and species to total larval fish fauna are only given when they exceed 0.1%. A: anadromous; E: estuarine; F: freshwater; O: marine estuarine-opportunist; S: marine straggler

Rank	Family/species	(Species Rank No.)	Total contribution: Family (%)	Total contribution: Species (%)	% by region: Lower	% by region: Middle	% by region: Upper	Total no.	Life-cycle category
1	Gobiidae		14 499 (88.2)						
	Pseudogobius olorum	(1)		8 756 (53.3)	1.2	12.5	61.4	36 013	E
	Arenigobius bifrenatus	(2)		5 128 (31.2)	3.4	38.0	32.5	20 817	E
	Gobiid 1	(4)		294 (1.8)		4.7	1.6	684	E
	Papillogobius punctatus	(6)		219 (1.3)	0.5	1.7	1.5	1 287	E
	Favonigobius lateralis	(11)		76 (0.5)	4.4	2.1	<0.1	417	O
	Gobiid 2	(25)		15 (0.1)	1.4			67	S
	Favonigobius suppositus	(34)		8			0.1	28	E
	Callogobius mucosus	(43)		3	0.2	0.1		13	S
2	Clupeidae		564 (3.4)						
	Nematalosa vlaminghi	(5)		269 (1.6)			1.9	1 351	A
	Hyperlophus vittatus	(7)		192 (1.2)	15.2	2.5		562	O
	Sardinella lemuru	(13)		62 (0.4)	5.8	0.2		194	S
	Sardinops neopilchardus	(18)		30 (0.2)	3.0	<0.1		128	S
	Clupeid 1	(39)		6	0.4	0.1		17	S
	Spratelloides robustus	(41)		4	0.4			28	O
	Etrumeus teres	(58)		1	0.1			4	S
3	Engraulididae		481 (2.9)						
	Engraulis australis	(3)		481 (2.9)	2.1	26.2	0.6	1 515	E
4	Blenniidae		157 (1.0)						
	Parablennius tasmanianus	(8)		142 (0.9)	7.3	4.1	0.1	600	E
	Omobranchus germaini	(25)		15 (0.1)	1.5	<0.1		73	S
5	Pinguipedidae		105 (0.6)						
	Parapercis haackei	(9)		105 (0.6)	10.1	0.1		410	S
6	Callionymidae		89 (0.5)						
	Callionymus goodladi	(10)		89 (0.5)	8.0	0.5		350	S
7	Carangidae		70 (0.4)						
	Pseudocaranx dentex	(12)		70 (0.4)	5.9	0.7		242	S
8	Atherinidae		65 (0.4)						
	Leptatherina wallacei	(20)		26 (0.2)		<0.1	0.2	107	E
	Atherinomorus ogilbyi	(22)		20 (0.1)	0.1	1.3	<0.1	98	O
	Leptatherina presbyteroides	(23)		19 (0.1)	0.8	0.7	<0.1	65	O
9	Syngnathidae		64 (0.4)						
	Urocampus carinirostris	(14)		54 (0.3)	0.1	2.6	0.1	248	E
	Stigmatopora nigra	(31)		9 (0.1)	0.8	<0.1		33	S
	Stigmatopora argus	(58)		1	0.1	<0.1		4	S
	Lissocampus runa	(70)		<0.5	<0.1			2	S
	Hippocampus angustus	(70)		<0.5	<0.1			1	S
	Vanacampus phillipi	(70)		<0.5	<0.1			1	S
10	Terapontidae		45 (0.3)						
	Pelates sexlineatus	(17)		36 (0.2)	3.4	0.1		159	O
	Amniataba caudavittatus	(31)		9 (0.1)		0.1	<0.1	31	E
11	Nemipteridae		43 (0.3)						
	Pentapodus vitta	(15)		43 (0.3)	4.1	0.1		174	S
12	Sillaginidae		42 (0.3)						
	Sillago spp.	(16)		42 (0.3)	4.0	0.1		168	O
13	Monacanthidae		30 (0.2)						
	Monacanthus chinensis	(28)		12 (0.1)	1.1			59	S
	Meushenia freycineti	(29)		11 (0.1)	1.0			41	S
	Acanthaluteres spilomelanurus	(43)		3	0.3			12	S
	Scobinichthys granulatus	(51)		2	0.2			10	S
	Monacanthid 2	(51)		2	<0.1	0.1		6	S
	Monacanthid 1	(70)		<0.5	<0.1			1	S
13	Apogonidae		30 (0.2)						
	Apogon rueppellii	(19)		28 (0.2)	0.1	0.5	0.1	165	E
	Apogonid	(51)		2	0.2			7	S

Table 1 (continued)

Rank	Family/species	(Species Rank No.)	Total contribution Family (%)	Species (%)	% by region Lower	Middle	Upper	Total no.	Life-cycle category
15	Gobiesocidae		25 (0.2)						
	Gobiesocid 2	(25)		15 (0.1)	1.4	0.1		58	S
	Gobiesocid 1	(37)		7	0.7	<0.1		28	S
	Gobiesocid 4	(43)		3	0.2	<0.1		12	S
	Gobiesocid 3	(58)		1	0.1			3	S
17	Cynoglossidae		18 (0.1)						
	Cynoglossus broadhursti	(24)		18 (0.1)	1.6	0.1		72	S
	Odacidae		11 (0.1)						
	Neoodax balteatus	(29)		11 (0.1)	1.1	<0.1		47	S
	Syphonognathes argyrophanes	(68)		0.5	<0.1			2	S
18	Labridae		11 (0.1)						
	Labridae Julidini	(34)		8	0.7	<0.1		28	S
	Labrid 1	(51)		2	0.2			8	S
	Labrid 2	(58)		1	0.1			4	S
	Clinidae		9 (0.1)						
	Cristiceps australis	(31)		9 (0.1)	0.8	0.1		34	S
20	Platycephalidae		9 (0.1)						
	Platycephalus endrachtensis	(37)		7	0.5	0.1	<0.1	31	E
	Platycephalus spp.	(51)		2	0.2	<0.1		10	S
22	Tripterygiidae		8 (0.1)						
	Lepidoblennius marmoratus	(34)		8 (0.1)	0.8			38	S
23	Pegasidae		6						
	Parapegasus natans	(39)		6	0.5	0.1		32	S
	Triglidae		5						
	Triglid	(43)		4	0.3			14	S
	Chelidonichthys kumu	(58)		1	0.1			6	S
24	Scorpaenidae		5						
	Gymnapistes marmoratus	(43)		3	0.2	0.1		13	S
	Scorpaenid	(51)		2	0.2			6	S
26	Sciaenidae		4						
	Sciaenid	(41)		4	0.4			16	S
	Bothidae		3						
	Arnoglossus sp.	(43)		3	0.3	<0.1		12	S
	Leptoscopidae		3						
27	*Lesueurina* sp.	(43)		3	0.2	<0.1		12	S
	Gerreidae		3						
	Gerres subfasciatus	(43)		3	0.2	<0.1		13	O
30	Pleuronectidae		2						
	Ammotretis elongatus	(51)		2	0.1	<0.1		7	S
	Sphyraenidae		1						
	Sphyraena obtusata	(58)		1	0.1			6	S
	Galaxiidae		1						
	Galaxias occidentalis	(58)		1			<0.1	4	F
31	Tetraodontidae		1						
	Tetraodontid	(58)		1	0.1			3	S
	Myctophidae		1						
	Lampadena sp.	(58)		1	0.1			1	S
	Soleidae		1						
	Strabozebrias cancellatus	(58)		1	<0.1			2	S
	Sparidae		0.5						
	Sparid	(68)		0.5	<0.1			3	S
36	Aulophidae		<0.5						
	Aulopus purpurissatus	(70)		<0.5	<0.1			1	S
38	Poecilidae		<0.5						
	Gambusia affinis	(70)		<0.5			<0.1	1	F
16	Unidentified			23 (0.1)	(2.0)	2.0	0.1	58	
Total (%)			16 432	16 432	1 024 (6.2)	1 451 (8.8)	13 957 (84.9)	66 814	

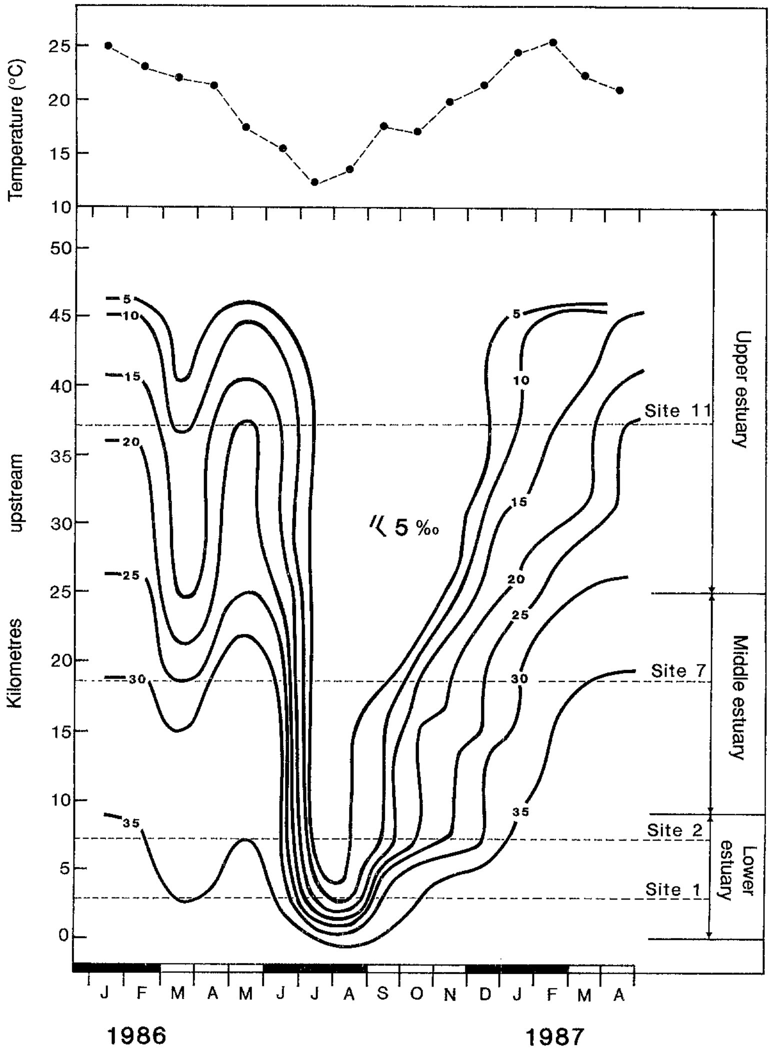

Fig. 2. Mean monthly surface temperatures (based on values for all 13 sites) and surface salinity in Swan Estuary between January 1986 and April 1987. Here and in Figs. 4–7 and Fig. 10, black and white bars on abscissa represent summer and winter months and autumn and spring months, respectively

Therefore, the monthly abundance variables were transformed into orthogonal polynomials using the CONTRAST subcommand. After examining the sphericity using Bartlett's test, modified univariate tests, using the Huynh-Feldt epsilon (Huynh and Feldt 1976), were applied to the polynomial coefficients. While the MANOVA subcommand CONTRAST will only allow full-order polynomials to be applied, the time-series data from each site were individually examined to determine the extent to which lower-order polynomials such as quadratics or cubics, could adequately fit the time-series trends. Since terms of order ≥ 8 were significant in the majority of sites, no attempt was made to reduce the order of polynomials in the repeated-measures analysis.

Classification was undertaken using the pattern analysis package (PATN) of Belbin (1987). These analyses, which employed the concentrations ($\log_{10} n+1$ transformed) of each of the 74 species caught as larvae, were used to investigate the degree to which the larval fish fauna at the various sites were dissimilar. The original species × site × time data set was reduced to a two-dimensional species × site matrix (74 × 13) by adding the concentration of each species over 12 mo. The values were then standardised using the range transformation option of PATN and transformed into a dissimilarity matrix using the Bray-Curtis measure of dissimilarity. This association matrix was subsequently employed for classification using flexible unweighted pair-group arithmetic averaging (UPGMA, $\beta = -0.1$) to construct the dendrogram (Belbin 1987). A Bray-Curtis percent dissimilarity value of 100 means complete dissimilarity and a value of 0 complete similarity. The contribution of each of the species to the classification produced by this technique was examined by the inspection of Cramer values generated by the GSTA procedure of PATN.

Results

Environmental conditions

Surface salinity in all three regions of the Swan Estuary underwent very pronounced seasonal changes between January 1986 and April 1987 (Fig. 2). The salinity throughout all but the upper reaches of the estuary declined from 20 to 35‰ in the autumn to <5‰ in mid-winter. This rapid decline in surface salinity in the winter of 1986 was due to a massive increase in freshwater discharge between June and August, particularly from the Avon River and, to a lesser extent, Ellen Brook (Waterways Commission of Western Australia personal communication). The rate at which salinity recovered in the spring was slower than that at which it had previously declined. For example, the salinity at Site 2 at the top end of the lower estuary fell from 35 to 5‰ in less than

8 wk, whereas it took ~5 mo to return to that of full-strength sea water (Fig. 2).

The overall mean surface water temperature throughout the estuary declined from 25.0 °C in January 1986 to a minimum of 12.6 °C in July, before increasing to a maximum of 25.5 °C in February 1987 (Fig. 2). Temperatures followed similar seasonal trends in all three regions of the estuary, but fluctuated to a greater extent in the upper than lower estuary (Fig. 5). Thus, mean monthly water temperatures ranged from 10.7 to 27.7 °C in the upper estuary and from 14.3 to 23.2 °C in the lower estuary.

Family and species composition

A total of 66 814 fish larvae, representing 37 families and 74 species, were collected from the 13 sampling sites in the Swan Estuary between January 1986 and April 1987 (Table 1). Of the 74 species distinguished during the study, 51 could be assigned to species, 5 to genus and 18 to family level. Unidentified larvae, comprising mainly yolk-sac larvae and damaged specimens, accounted for only 0.1% of the total number caught (Table 1).

The 8 identified species recorded for the Gobiidae, the 7 for the Clupeidae and the 6 for both the Syngnathidae and Monacanthidae were the maximum for any family (Table 1). The Gobiidae was by far the most abundant family, comprising 88.2% of the total number of larvae, followed by the Clupeidae (3.4%), Engraulididae (2.9%) and Blenniidae (1.0%) (Table 1). The only two other families which contributed more than 0.4% were the Pinguipedidae (0.6%) and Callionymidae (0.5%).

The most abundant species were the gobies *Pseudogobius olorum* and *Arenigobius bifrenatus*, which accounted for 53.3 and 31.2% of the total, respectively. These species were followed in order of relative abundance by *Engraulis australis* (2.9%), *Nematalosa vlaminghi* (1.6%), *Papillogobius punctatus* (1.3%), *Hyperlophus vittatus* (1.2%) and *Parablennius tasmanianus* (0.9%) (Table 1). The larvae of *Favonigobius lateralis, Sardinella lemuru, Sardinops neopilchardus, Parapercis haackei, Callionymus goodladi, Pseudocaranx dentex, Leptatherina wallacei, Urocampus carinirostris, Pelates sexlineatus, Pentapodus vitta* and *Apogon rueppellii* each contributed between 0.2 and 0.6% (Table 1).

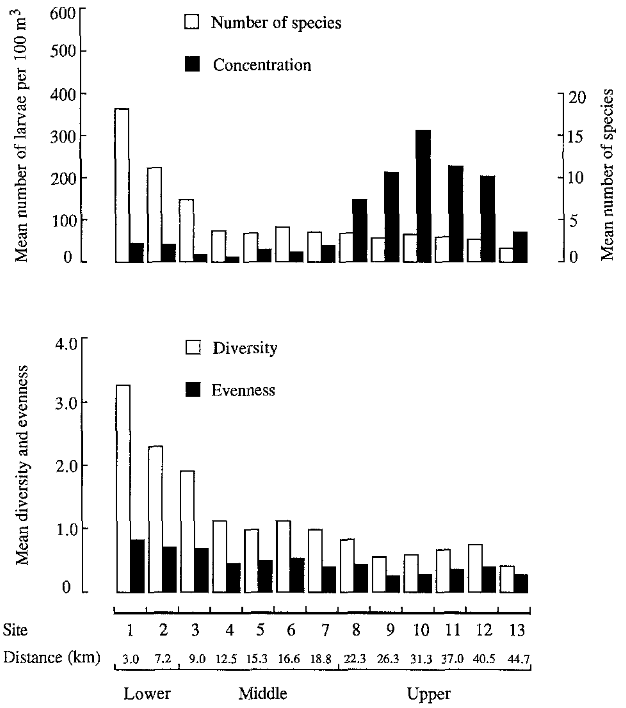

Fig. 3. Mean number of species, concentration (i.e., nos/100 m³), species diversity (*H*') and evenness (*J*) for samples of fish larvae collected at each site in lower, middle and upper Swan Estuary during study period. Here, and in Figs. 8 and 9, lower abscissa shows distance from estuary mouth to respective sampling site

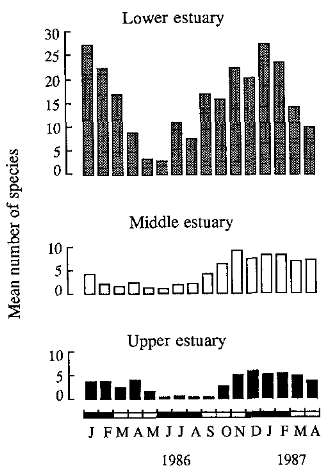

Fig. 4. Mean number of species in the lower, middle and upper Swan Estuary in each month between January 1986 and April 1987

Number of species, concentration of larvae and diversity

The mean monthly concentrations of larvae were far greater at sites in the upper estuary than at those in the lower estuary, whereas the reverse was true for the mean number of species (Fig. 3). The respective mean larval concentrations for sites in the upper and lower estuary were 197 and 42 larvae per 100 m³, whereas the respective mean numbers of species in these two regions were 2.7 and 14.7. The mean monthly concentration of larvae at the different sites ranged from 10.7 larvae per 100 m³ at Site 4 in the middle estuary to 313.9 larvae per 100 m³ at Site 10 in the upper estuary. Mean number of species ranged from 1.7 at Site 13 in the upper estuary to 18.2 at Site 1 in the lower estuary. The monthly mean values for diversity (*H*') and evenness (*J*) were greatest in the lower estuary and decreased with distance from the estuary mouth, the decline being most pronounced over the first 12.5 km of the estuary (Fig. 3).

Seasonal trends in number of species and concentration of larvae

The mean number of species followed the same seasonal trend in each of the three regions of the estuary, reaching a maxima between the middle of spring (October) and end of summer (February) and declining to a minimum during winter (June to August) (Fig. 4). The maximum

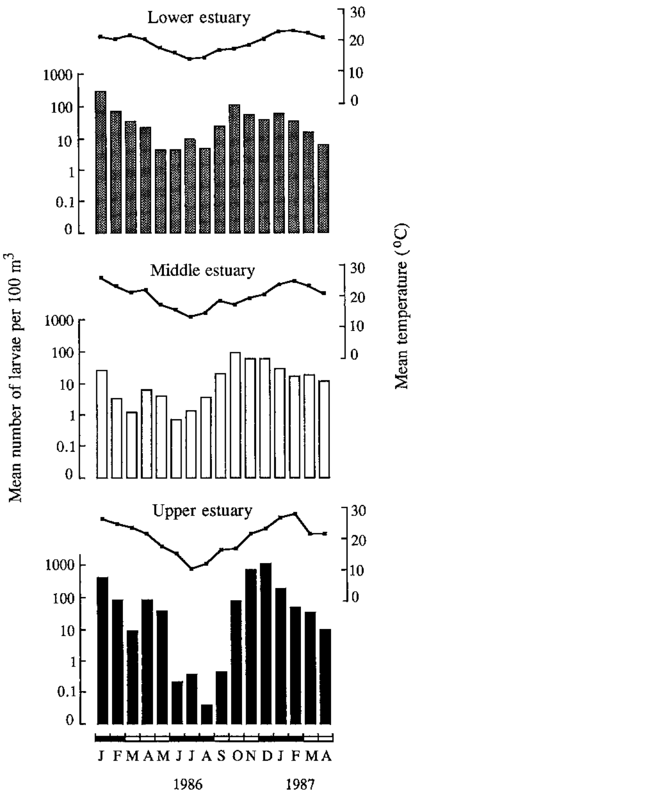

Fig. 5. Mean concentration of fish larvae in the lower, middle and upper Swan Estuary in each month between January 1986 and April 1987. Mean monthly surface temperatures for each region are also shown

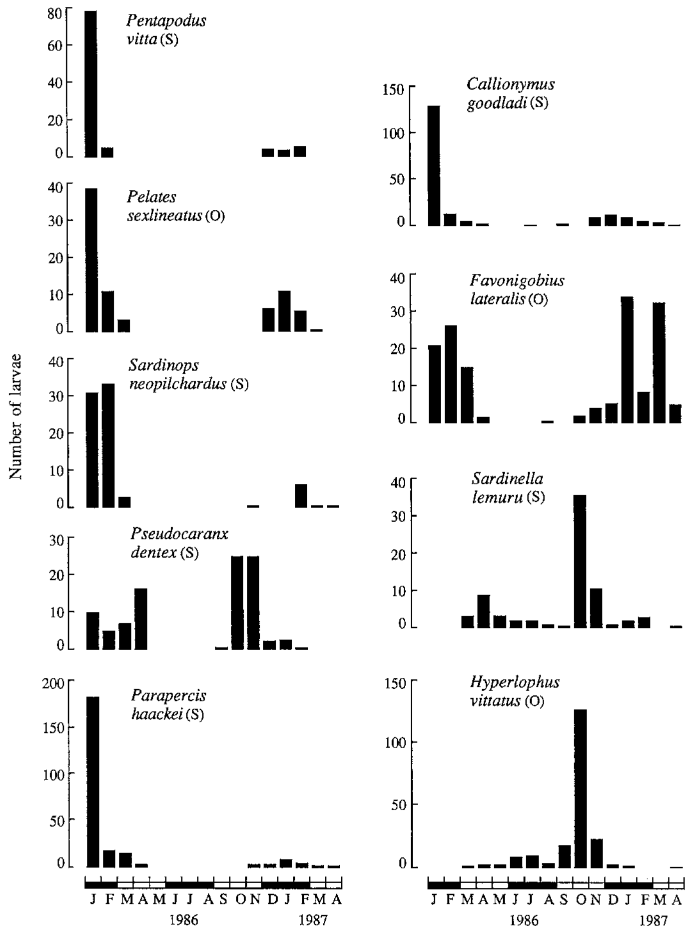

Fig. 6. Numbers of larvae of six most abundant marine stragglers (S) and three most abundant marine estuarine-opportunits (O) recorded throughout Swan Estuary in each month between January 1986 and April 1987. Data here and in Figs. 7–9 are sum of number of larvae in each sample after the values for each sample have been standardised to volume of 100 m^3

mean monthly number of species recorded in the lower estuary (27.5) was far greater than in either the middle (7.2) or upper estuary (5.2).

The mean concentration of larvae also followed similar seasonal trends in each of the three regions of the estuary (Fig. 5). Thus, mean concentrations of larvae in each region fell from high levels during the summer of 1986 to a low level during the winter, before rising again in the following spring and summer and then declining in the autumn. During the period between May 1986 and April 1987, the maximum mean monthly concentrations of larvae in the lower and middle estuary (108 and 90 per 100 m^3) and in the upper estuary (1111 per 100 m^3) were recorded in October and December, respectively. The decline that occurred in the larval concentrations in all three regions of the estuary between June and August was most pronounced in the upper estuary (Fig. 5), with very few larvae being caught in that region in August when freshwater discharge was at its maximum and salinities were therefore at their minimum (Fig. 2). Although mean monthly concentrations of larvae in each region of the estuary followed a similar seasonal trend to that of mean surface temperature, larval concentrations reached a peak between 2 and 4 mo earlier than temperature (Fig. 5).

Seasonal occurrence of abundant species

Most of the species found as larvae during this study were caught either exclusively or predominantly between September and March, with peak numbers of most of the abundant species occurring between October and January, i.e., between the middle of spring and end of summer (Figs. 6, 7). While the larvae of the marine species such as *Pentapodus vitta*, *Pelates sexlineatus* and *Sardinops neopilchardus* occurred over a relatively restricted period of time, those of other marine species such as *Favonigobius lateralis*, *Sardinella lemuru* and *Hyperlophus vittatus* were caught in most months of the year (Fig. 6).

Larvae of the estuarine species *Leptatherina wallacei*, *Parablennius tasmanianus*, *Urocampus carinirostris*, *Engraulis australis*, *Arenigobius bifrenatus* and *Pseudogobius olorum* were collected over a protracted period and each reached peak numbers between October and April (Table 2, Fig. 7). By contrast, the larvae of two other estuarine species, *Apogon rueppellii* and the anadromous *Nematalosa vlaminghi*, were caught in only four months of the year (Fig. 7). In the case of *Papillogobius punctatus*, which occurred in six months of the year, >90% of the larvae were caught in January in both years. The numbers of *N. vlaminghi* larvae varied greatly between years, with the values for January and February being much lower in 1986 than in 1987 (Fig. 7).

Table 2. Location (sites and distance from estuary mouth) where collectively at least 80% of the larvae of the most abundant species in the different life-cycle categories were found, percentage of catch of each of the species in the regions of the estuary where they were caught, and peak months of occurrence

Species	Sites	Distance from: Estuary mouth (km)	Percentage in:			Peak months
			Lower estuary	Middle estuary	Upper estuary	
Stragglers						
Callionymus goodladi	1– 2	3.0– 7.2	96.7	3.3	0.0	Nov.–Feb.
Parapercis haackei	1– 2	3.0– 7.2	99.6	0.4	0.0	Dec.–Mar.
Pentapodus vitta	1– 2	3.0– 7.2	99.0	1.0	0.0	Dec.–Feb.
Sardinops neopilchardus	1– 2	3.0– 7.2	98.7	1.3	0.0	Jan.–Feb.
Pseudocaranx dentex	1– 2	3.0– 7.2	93.7	6.3	0.0	Oct.–Jan.
Sardinella lemuru	1– 2	3.0– 7.2	98.0	2.0	0.0	Oct.–Apr.
Opportunists						
Pelates sexlineatus	1– 2	3.0– 7.2	98.8	1.2	0.0	Dec.–Feb.
Hyperlophus vittatus	1– 2	3.0– 7.2	91.5	8.5	0.0	Sep.–Nov.
Favonigobius lateralis	1– 7	9.0–18.8	78.0	21.5	0.5	Dec.–Mar.
Estuarine						
Parablennius tasmanianus	1– 7	3.0–18.8	73.5	23.8	2.7	Oct.–Mar.
Engraulis australis	3– 8	9.0–22.3	10.5	76.1	13.4	Oct.–Dec.
Urocampus carinirostris	5– 9	15.3–26.3	4.7	70.1	25.2	Nov.–Apr.
Pseudogobius olorum	7–13	22.3–44.7	0.4	2.5	97.1	Nov.–Jan.
Arenigobius bifrenatus	7–12	22.3–40.5	1.9	12.5	85.6	Oct.–Jan.
Papillogobius punctatus	9–10	26.3–31.3	6.4	12.8	80.8	Jan.–Mar.
Apogon rueppellii	7–11	18.8–37.0	9.6	26.8	63.6	Dec.–Feb.
Leptatherina wallacei	10–13	31.3–44.7	0.0	4.6	95.4	Nov.–Apr.
Anadromous						
Nematalosa vlaminghi	10–12	31.3–40.5	0.0	0.0	100.0	Nov.–Jan.

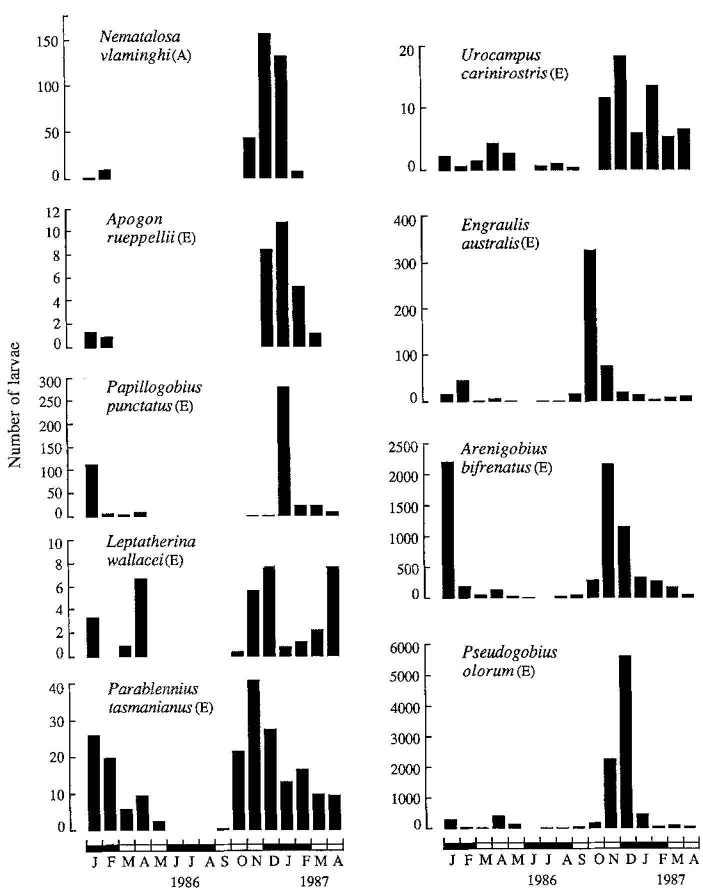

Fig. 7. Numbers of larvae of eight most abundant estuarine species (E) and the sole anadromous species (A) recorded throughout Swan Estuary in each month between January 1986 and April 1987

Spatial distribution of abundant species

The larvae of each of the six most abundant species of marine straggler (*Callionymus goodladi*, *Parapercis haackei*, *Pentapodus vitta*, *Sardinops neopilchardus*, *Pseudocaranx dentex* and *Sardinella lemuru*), and of the three most abundant species of marine estuarine-opportunist (*Pelates sexlineatus*, *Hyperlophus vittatus* and *Favonigobius lateralis*), were found predominantly in the lower estuary (Table 2, Fig. 8). By contrast, the larvae of all estuarine species (except *Parablennius tasmanianus*), and those of the single anadromous species occurred mainly at sites in either the middle estuary (e.g. *Engraulis australis* and *Urocampus carinirostris*) or upper estuary (e.g. *Pseudogobius olorum*, *Arenigobius bifrenatus*, *Papillogobius punctatus*, *Apogon rueppellii*, *Leptatherina wallacei* and *Nematalosa vlaminghi*) (Table 2, Fig. 9).

The above generalisations regarding the six species of marine straggler and the marine estuarine-opportunists *Pelates sexlineatus* and *Hyperlophus vittatus* are illustrated by the observation that between 91.5 and 99.6% of the larvae of these species were collected at Sites 1 and 2 in the lower estuary (Table 2). Moreover, five of these species were not collected upstream of Site 3, which is locat-

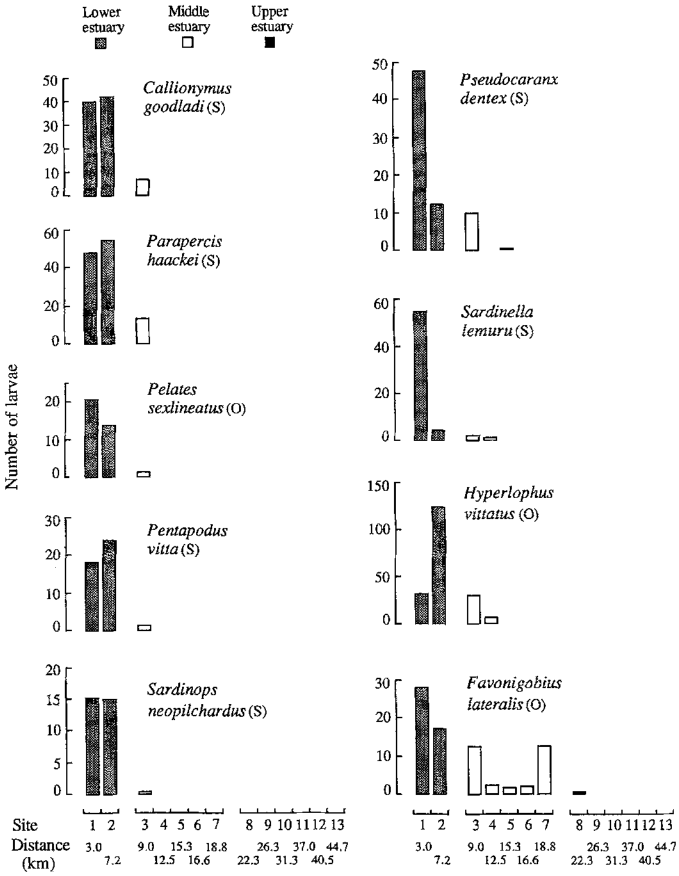

Fig. 8. Numbers of larvae of six most abundant marine stragglers (S) and three most abundant marine estuarine-opportunists (O) at sites in lower middle and upper Swan Estuary throughout study period

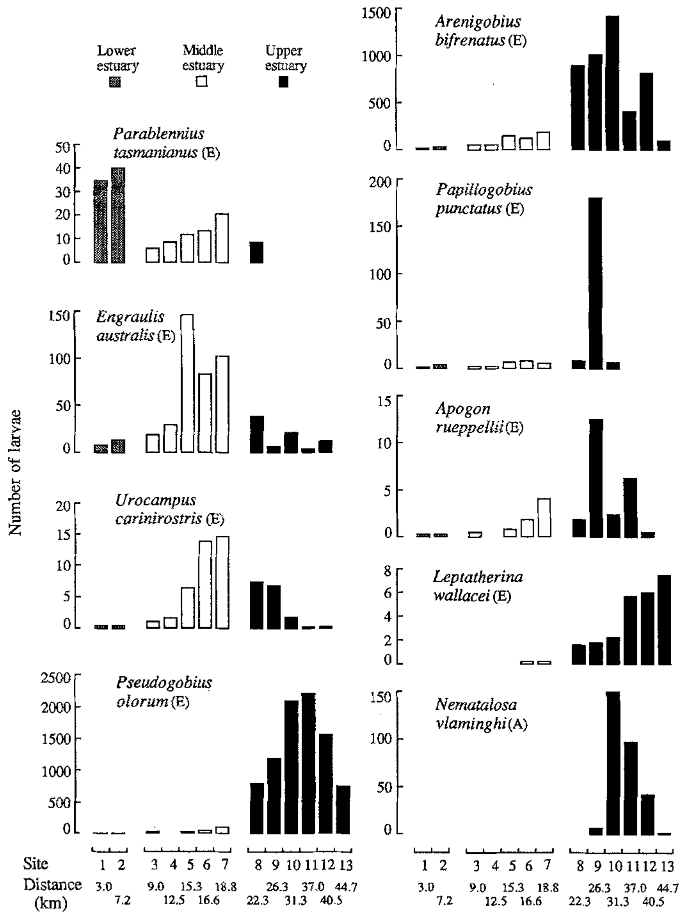

Fig. 9. Numbers of the larvae of eight most abundant estuarine species (E) and the sole anadromous species (A) at sites in lower, middle and upper Swan Estuary throughout study period

ed 9.0 km from the estuary mouth (Table 2, Fig. 8). Although the larvae of *Favonigobius lateralis* were caught predominantly in the lower estuary (78.0%), they were also found in the middle estuary (21.5%) and, exceptionally, at Site 8 in the upper estuary (Fig. 8).

Over 80% of the larvae of estuarine species such as *Pseudogobius olorum*, *Arenigobius bifrenatus*, *Leptatherina wallacei* and *Papillogobius punctatus* were caught in the upper estuary (Table 2). In the case of *P. punctatus*, most larvae were almost exclusively caught at Site 9 in the upper estuary (Fig. 9). All larvae of the anadromous *Nematalosa vlaminghi* were caught in the upper estuary, and of these >95% were collected at Sites 10, 11 and 12, which are located between 31.3 and 40.5 km from the estuary mouth.

Over 70% of the larvae of the estuarine species *Engraulis australis* and *Urocampus carinirostris* were collected in the middle estuary (Table 2, Fig. 9). Although the larvae of the estuarine species *Apogon rueppellii* were most abundant in the upper estuary, nearly 27% of all the larvae of this species were caught in the middle estuary.

Interrelationships between spatial and seasonal trends in *Pseudogobius olorum*

When orthogonal polynomials were fitted in the region × month repeat-measures analysis of variance of the data on the concentration of larval *Pseudogobius olorum*, the 1st to 4th, 6th, 8th and 10th orthogonal polynomial coefficients were found to be significant over the time effect. This indicates that a seven-term polynomial expression adequately described the monthly variation in catch. The polynomial coefficients are not presented, since they do not have any biological meaning. Of the region × time tests of each polynomial coefficient, only the 4th and 6th proved significant ($P<0.001$ and $P<0.01$, respectively), indicating that although region × time differences were present, they were not marked. This view is confirmed by the similarity in the seasonal trends generally shown by *P. olorum* in the different regions of the estuary (Fig. 10).

Classification

Classification of the abundance of all 74 species caught as larvae at the different sites separated the data into three distinct groups (Fig. 11). These groups corresponded respectively to the sites in the lower (1, 2), middle (3–7) and upper (8–13) estuary. The group containing the two sites in the lower estuary was almost completely dissimilar from the groups containing the sites in the middle and upper estuary. The sites in the latter two regions of the estuary fused at approximately the 60% level of dissimilarity. All sites within each of the three regions of the

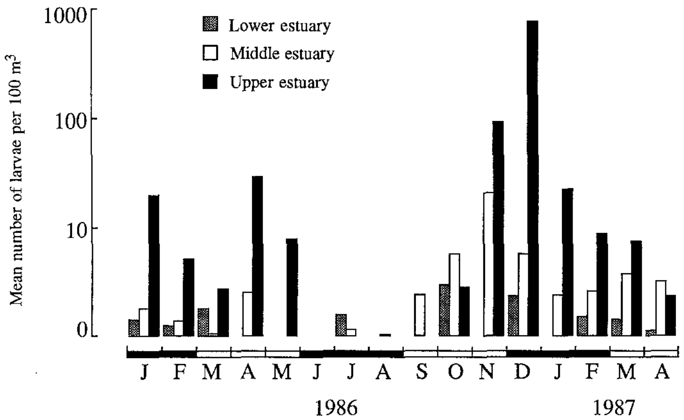

Fig. 10. *Pseudogobius olorum.* Mean concentration of larvae in lower, middle and upper Swan Estuary between January 1986 and April 1987

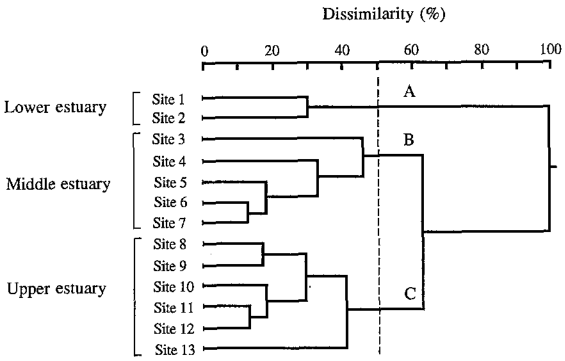

Fig. 11. Classification using abundance of all species caught as larvae at all 13 sampling sites in Swan Estuary. Scale on dendrogram corresponds to Bray-Curtis dissimilarity coefficient

estuary fused at a level below 50% dissimilarity, with Sites 6 and 7 in the middle estuary and Sites 11 and 12 in the upper estuary showing the lowest levels of dissimilarity (>20%). Since the Cramer values for the two most abundant species, i.e., *Pseudogobius olorum* and *Arenigobius bifrenatus*, ranked 20th and 38th respectively, amongst those of all species used for the classification shown in Fig. 11, this classification was not dominated by data for these two species.

Contribution of life-cycle categories

Of the 74 teleost species, 51 (i.e., 68.9%) recorded as larvae in the Swan Estuary were marine stragglers. Of the remaining species , 12 were estuarine, 8 were marine estuarine-opportunists, 2 were freshwater and 1 was anadromous. The total number of species declined from 67 in the lower estuary to 43 in the middle estuary to 18 in the upper estuary (Table 3). In terms of number of species, the larvae of marine stragglers and marine estuarine-opportunists dominated the assemblage in the lower estuary, whereas the larvae of estuarine species dominated that of the upper estuary.

The larvae of the 51 species of marine stragglers were all recorded in the lower estuary, but never in the upper estuary. Species of marine stragglers accounted for 76.2 and 58.1% of the total number of species recorded in the lower and middle estuary, respectively (Table 3). The larvae of each of the 8 marine estuarine-opportunist species were found in the lower estuary and of these 7 occurred in the middle estuary and 3 in the upper estuary (Table 3). The larvae of each of the 12 estuarine species caught during the study were recorded in the upper estuary and 11 and 8 of these were collected in the middle and lower

Table 3. Number of species and larvae, and percentage contribution of each life-cycle category to total numbers recorded in whole Swan Estuary and its three main regions

Life-cycle category	Whole estuary		Region of estuary					
			Lower		Middle		Upper	
	N	(%)	*N*	(%)	*N*	(%)	*N*	(%)
Number of species								
Stragglers	51	(68.9)	51	(76.2)	25	(58.1)	0	(0.0)
Opportunists	8	(10.8)	8	(11.9)	7	(16.3)	3	(16.6)
Estuarine	12	(16.2)	8	(11.9)	11	(25.6)	12	(66.6)
Anadromous	1	(1.4)					1	(5.6)
Freshwater	2	(2.7)					2	(11.2)
Total	74		67		43		18	
Number of larvae								
Stragglers	619	(3.8)	580	(56.7)	39	(2.7)	0	(0.0)
Opportunists	392	(2.4)	290	(28.3)	99	(6.8)	3	(<0.1)
Estuarine	15 151	(92.2)	154	(15.0)	1 313	(90.5)	13 684	(98.0)
Anadromous	269	(1.6)					269	(1.9)
Freshwater	1	(<0.1)					1	(<0.1)
Total	16 432		1 024		1 451		13 957	

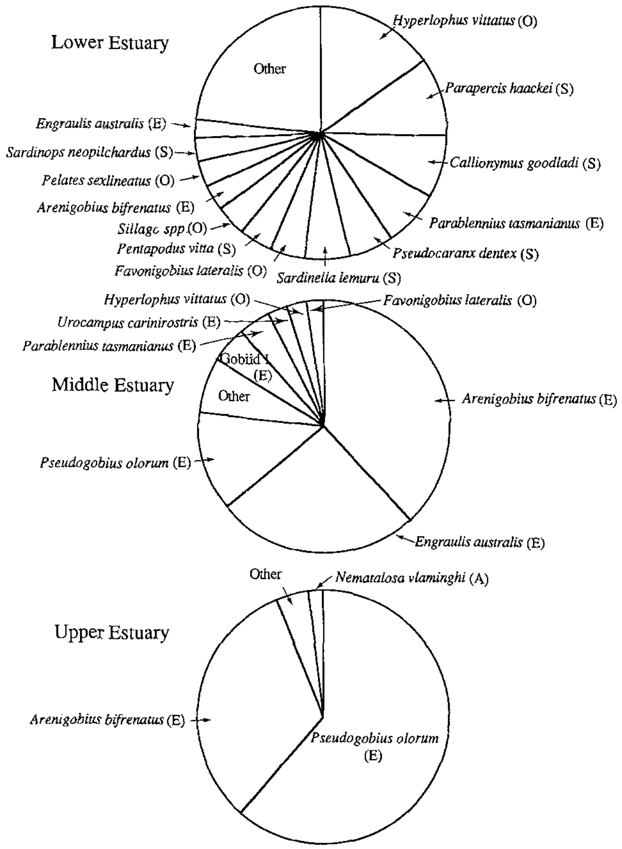

Fig. 12. Relative contributions of larvae of most abundant species of marine stragglers (S), marine estuarine-opportunists (O) and the estuarine (E) and anadromous (A) categories to the assemblages in lower, middle and upper Swan Estuary throughout study period

estuary, respectively. Larvae of *Nematalosa vlaminghi*, the only representative of the anadromous category, and also of *Galaxias occidentalis* and *Gambusia affinis*, the only freshwater species collected during the study, were restricted to the upper estuary (Tables 1, 3).

The number of larvae representing the marine straggler category accounted for 56.7% of the total in the lower estuary and only 2.7% in the middle estuary (Table 3). The contribution of the number of larvae of marine estuarine-opportunistic species fell from 28.3% in the lower estuary to 6.8% in the middle estuary to >0.1% in the upper estuary. The most abundant larvae in the lower estuary were those of the marine estuarine-opportunist *Hyperlophus vittatus* and of the marine stragglers *Parapercis haackei* and *Callionymus goodladi* (Fig. 12). Overall, the larvae of marine stragglers and estuarine opportunists accounted, respectively, for only 3.8 and 2.4% of the total number of larvae caught throughout the whole estuary (Table 3).

Of the total numbers of larvae, 92% belonged to species which spawned within the estuary. They comprised >90% of the total in both the middle and upper estuary, but only 15.0% of the numbers in the lower estuary (Table 3). The fact that the gobiids *Pseudogobius olorum* and *Arenigobius bifrenatus* collectively comprised 93.9% of the larvae caught in the upper estuary accounts for the dominance of the Gobiidae in this region of the estuary (Table 1, Fig. 12). These two gobiids were also abundant in the middle estuary and, together with *Engraulis australis*, accounted for 76.7% of the catch in that region. The single anadromous species (*Nematalosa vlaminghi*) contributed 1.9% to the total number of larvae in the upper estuary. The larvae of the two freshwater species (*Galaxias occidentalis* and *Gambusia affinis*) were present in very low numbers in the upper estuary (Tables 1, 3).

Discussion

Faunal composition

The larval assemblage of the Swan Estuary was overwhelmingly dominated by the Gobiidae during the present study. Thus, 4 species of gobies ranked amongst the 6 most abundant species and the family collectively accounted for >88% of the fish larvae caught within the system. The major contribution made by the Gobiidae to the larval assemblage of the Swan Estuary parallels the situation found in many estuaries and protected inshore marine waters elsewhere in the Southern Hemisphere and also in the Northern Hemisphere (e.g. Pearcy and Myers 1974, Melville-Smith and Baird 1980, Miller 1984, Beckley 1986, Steffe and Pease 1988, Steffe 1989). The Clupeidae, which was second in terms of number of species (7) and total abundance, also frequently contributes greatly to the larval assemblages of many estuaries (Pearcy and Richards 1962, Pearcy and Myers 1974, Melville-Smith and Baird 1980, Beckley 1986). The Engraulididae, Blenniidae, Pinguipedidae, Callionymidae and Carangidae, which ranked 3rd to 7th in terms of abundance in the Swan Estuary, were represented by only one species in all cases except the Blenniidae, which was represented by two species.

Spatial and seasonal trends

The data presented in this paper provide overwhelming evidence that the larvae of various species found within the Swan Estuary are each largely concentrated in certain regions of the estuary and in certain months of the year. In this context, it is particularly significant that the community variables (e.g. number of species and species diversity) and the abundance of most species show a marked and consistent tendency to decline with increasing distance from the site of maximum numbers and with increasing time from the month of maximum numbers. The fact that most species show such a marked tendency to occur within a particular area of the estuary and at a particular time of the year, obviated the need for the use of statistical treatment to verify these distribution patterns. Indeed, the large number of site × month zero counts produces a situation in which the underlying assumptions of analysis of variance and other less restricted linear models are not met. Furthermore, repeated-measures analysis of variance of the one abundant species (*Pseudogobius olorum*), which was found at 12 of the 13 sites and in all but one month of the year, showed that the temporal trends in concentration within the various regions were similar.

The observation that the mean concentration of fish larvae in each of the three regions of the Swan Estuary reached a maximum in late spring/early summer, 2 to 4 mo before the attainment of maximum temperatures, parallels the situation found in temperate estuaries and marine embayments, such as Algoa Bay in South Africa (Beckley 1986), Whangateau Harbour in New Zealand (Roper 1986), Port Phillip Bay in south-eastern Australia (Jenkins 1986), and Botany Bay on the east coast of Australia (Steffe and Pease 1988). The high overall concentrations in the late spring and early summer were due to the presence at that time of large numbers of the larvae of such relatively abundant species as *Pseudogobius olorum*, *Arenigobius bifrenatus*, *Nematalosa vlaminghi*, *Engraulis australis*, *Parablennius tasmanianus*, *Pseudocaranx dentex* and *Urocampus carinirostris*.

Although all species tended to peak in abundance at a particular time of the year, some of these species, including the clupeids *Hyperlophus vittatus* and *Sardinella lemuru* and the gobies *Pseudogobius olorum*, *Arenigobius bifrenatus* and *Favonigobius lateralis*, were caught throughout much of the year. In the case of the gobies, this result is consistent with the observation that mature individuals of these three gobiid species have been caught in the Swan Estuary in most months of the year (H. S. Gill unpublished data). Such protracted spawning periods are typical of many gobiid species throughout the world (Darcy 1980). The lengthy period over which the larvae of *Leptatherina wallacei* were found is consistent with the fact that this species spawns continuously between late spring and early autumn (Prince and Potter 1983).

In contrast to the larvae of the above gobiids and clupeids and also of *Leptatherina wallacei*, the larvae of *Papillogobius punctatus*, *Nematalosa vlaminghi* and *Apogon rueppellii* were found in only a few months. The occurrence of the larvae of *N. vlaminghi* and *A. rueppellii* between late spring and mid-summer is consistent with the period during which these species are known to spawn in the Swan Estuary (Chubb and Potter 1984, Chrystal et al. 1985).

The trends shown by the larvae of four of the less abundant species (*Gymnapistes marmoratus*, *Lesueurina* sp., *Ammotretis elongatus* and *Galaxias occidentalis*), were atypical in that their peak number occurred between the winter and early spring (see also Neira 1989, Neira and Gaughan 1989). The months when the larvae of *Gymnapistes marmoratus* were found coincides with the spawning period reported for this species in Tasmania (Grant 1972), and in Port Phillip Bay (Jenkins 1986) and the Gippsland Lakes (Ramm 1986) in south-eastern mainland Australia.

Number of species, larval concentrations and diversity within regions of the estuary

The number of species was by far the greatest at the site closest to the estuary mouth, a feature which reflects the presence of many marine species. The sharp decline in the number of species over the first 12.5 km of the estuary reflects the restricted penetration of the estuary by many of these species. A high species diversity has also been reported for the ichthyoplankton at or near the mouth of estuaries elsewhere in the world (Pearcy and Richards 1962, Crocker 1965, Pearcy and Myers 1974, Misitano 1977, Miskiewicz 1987, Steffe and Pease 1988). The marked increase in the mean concentration of the larvae in the upper estuary, which contrasts with the above trends shown by the number of species, is due to the very large number of larvae produced by the relatively small number of species that spawn in that region of the estuary. The combination of a decrease in the number of species and an increase in dominance by a few species in an upstream direction accounts for the progressive decline in diversity throughout the length of the estuary.

Classification performed on the concentration of each of the 74 species collected as larvae at each of the sites clearly separated the sites in the lower, middle and upper regions of the estuary, with those in the lower estuary being particularly discrete. This clear distinction reflects the dominance of marine-spawned larvae in the lower estuary and of estuarine-spawned larvae in both the middle and upper estuary.

Contribution of marine-spawned larvae

Approx 80% of the species recorded as larvae throughout the Swan Estuary belonged to species which typically spawn in marine waters (cf. Table 1 and Potter et al. 1990). The number of marine species declined markedly in an upstream direction, with no marine stragglers and only three marine estuarine-opportunists penetrating the upper estuary. This decline is reflected by the fact that the contribution of the numbers of larvae of these marine species to the total numbers in the different regions of the estuary fell from 85% in the lower estuary to 9.5% in the middle estuary and <0.1% in the upper estuary.

The restriction of the larvae of marine stragglers to the lower Swan Estuary is emphasized by the fact that between 93.7 and 99.6% of the larvae of each of the six most abundant species in this category were recorded in this region. Although 91.5 and 98.8% of the larvae of two of the three most abundant marine estuarine-opportunists (*Hyperlophus vittatus* and *Pelates sexlineatus*, respectively) were likewise recorded in the lower estuary, 21.5% of the larvae of the third most abundant representative of this category (*Favonigobius lateralis*) were obtained in samples from the middle estuary. This implies that this latter abundant and typically marine gobiid species may sometimes spawn within the main body of the estuary.

The restriction to the lower estuary of the vast majority of the larvae of all marine species is consistent with the observation that their numbers decline markedly between Fremantle Harbour at the mouth of the estuary and the top end of the lower estuary (Gaughan et al. 1990). The very low numbers of the larvae of these marine species in the middle estuary and their virtual absence above Site 4, which is located 12.5 km from the estuary mouth, is almost certainly associated with the greatly attenuated effect of the small daily tides characteristic of the southwestern Australian coast (Hodgkin and Di Lollo 1958) on the wide basins of the middle Swan Estuary.

While there is some evidence that *Hyperlophus vittatus* enters the Swan Estuary as larvae and is transported upstream through the lower estuary by tidal action (Gaughan et al. 1990), this is not the case with other abundant species of marine estuarine-opportunists. For example, the mugilids *Mugil cephalus* and *Aldrichetta forsteri* and the tetraodontid *Torquigener pleurogramma*, which are very abundant as juveniles and adults in the Swan Estuary (Chubb et al. 1981, Potter et al. 1988), were never caught as larvae during the current study. Although it is possible that the larvae of these species could have been entering the estuary along the bottom, it is probably relevant that they were also not caught during the study of Gaughan et al. (1990), which utilized oblique tows. Furthermore, the minimum length at which *M. cephalus* and *A. forsteri* are first caught within the Swan Estuary (18.0 to 33.0 mm; Chubb et al. 1981, Potter et al. 1988) is greater than at which they transform (Leis and Trnski 1989, Neira unpublished data), which indicates that these species enter this system predominantly as juveniles. The recruitment of these two mugilid species into the estuary as juveniles parallels the situation with many other mugilids in estuaries elsewhere in the world (De Silva 1980, Claridge and Potter 1985, Blaber 1987).

Contribution of estuarine-spawned larvae

Although only 12 of the 74 species recorded as larvae during the current study complete their life cycle within the Swan Estuary, they contributed 92.2% to the total numbers of larvae caught at the 13 sites throughout the estuary. Their high numbers were largely due to the presence of the larvae of three gobiid species (*Pseudogobius olorum*, *Arenigobius bifrenatus* and *Papillogobius punctatus*) and one species of anchovy (*Engraulis australis*). When the larvae of the anadromous species *Nematalosa vlaminghi* were included, the contribution of larvae which have been spawned in the estuary to the total larval assemblage increased to 93.6%.

The numbers of larvae of 12 of the 13 species which spawn within the estuary were greatest in either the middle and/or upper estuary. The upper estuarine regions where the larvae of *Nematalosa vlaminghi* and *Leptatherina wallacei* were collected correspond to the areas where these species spawn (Prince et al. 1983, Chubb and Potter 1984). The relatively large numbers of *Engraulis australis* larvae at sites in the middle and upper estuary between 9.0 and 22.3 km from the estuary mouth is also consistent with the location where the majority of the juveniles and adults of this species are found (Loneragan et al. 1989). This species of anchovy also breeds in estuaries elsewhere in Australia and over a very protracted period (Blackburn 1950, Arnott and Mackinnon 1985, Ramm 1986). The capture of most of the *Pseudogobius olorum* larvae in the upper and middle estuary is consistent with the distribution of the juveniles and adults of this gobiid (Loneragan et al. 1989).

The Gobiidae, which accounted for >95% of the total number of larvae belonging to estuarine-spawning species, deposit demersal adhesive eggs (Leis and Rennis 1983, Miller 1984). Families such as the Blenniidae and Atherinidae, which also contain species that spawn within the Swan Estuary, likewise produce demersal eggs (Leis and Rennis 1983, White et al. 1984). The eggs of representatives of most of the teleosts that spawn in Northern Hemisphere estuaries also tend to be demersal and their larvae typically dominate the larval fish assemblages of those systems (Pearcy and Richards 1962, Crocker 1965, Chenoweth 1973, Pearcy and Myers 1974, Able 1978, Cowan and Birdsong 1985, Johnston and Morse 1988). The dominance of larvae hatched from demersal eggs in the Swan Estuary parallels the situation elsewhere in the Southern Hemisphere, such as in the Swartkops Estuary in South Africa and in Botany Bay in eastern Australia (Melville-Smith and Baird 1980, Steffe and Pease 1988, Steffe 1989). The possession of demersal and adhesive eggs by these species would help reduce their potential loss from the estuary with the seaward flow, thus increasing the chances of the larvae being retained within the estuary (Able 1978, Johnston and Morse 1988). Epibenthic schooling, as in the case of flexion and postflexion larvae of *Leptatherina presbyteroides*, is also considered an important mechanism for larval retention within estuaries (Steffe 1990).

Parental care and other reproductive specializations are also employed by some of the teleosts which breed within the Swan Estuary. For example, the eggs of the gobiids *Arenigobius bifrenatus* and *Favonigobius lateralis* are guarded by the parents until the young are hatched (H. S. Gill personal communication), as in many other species of gobies (Darcy 1980). Oral brooding, as in *Apogon rueppellii* (Chrystal et al. 1985, Neira 1991), and pouch-brooding, as in *Urocampus carinirostris* and most other syngnathids (Fritzsche 1984), allow the young to be released at an advanced stage of development and thereby reduce their chances of being flushed downstream.

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