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The ichthyoplankton of a seasonally closed estuary in temperate Australia. Does an extended period of opening influence species composition?

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Fish eggs and larvae were collected monthly between September 1987 and April 1989 from sites throughout the main basin and within the saline regions of the two main tributary rivers of Wilson Inlet, a seasonally closed estuary in south-western Australia. Of the eggs, 43·7% belonged to *Engraulis australis* (Shaw) and the rest to unidentified teleosts. The larval fish assemblage comprised 17 families represented by 25 species. The Gobiidae contained the highest number of species (four) and contributed approximately 57% of all larvae caught. *Pseudogobius olorum* (Sauvage) and *E. australis* were the most abundant species, contributing 43·9 and 27·9% to the total larval catch, respectively. The larvae of species which breed within Wilson Inlet dominated the assemblage, both in terms of number of species (64%) and contribution to total catch (99·9%). The numbers of the eight marine species and one freshwater species represented in the ichthyoplankton were very low. Classification and multi-dimensional scaling ordination showed that the composition of the larval fish fauna at the various sites during a period when the estuary remained open to the sea (December 1988–April 1989) was similar to that of the corresponding sites during the same period in the previous year when the estuary had become closed (December 1987–April 1988). This can be attributed to the spatial distribution, time of occurrence and abundance of estuarine-spawned larvae being similar in the two periods and to the rarity of marine-spawned larvae, even in the spring and summer of 1988/1989 when the estuary was open for the whole time when most marine teleosts spawn in south-western Australia. The low occurrence of marine-spawned larvae in Wilson Inlet reflects the fact that tidal water movement within the basin of the system is so small that it is unable to facilitate the transport and dispersion of larvae. The ichthyoplankton of Wilson Inlet resembles that of other poorly-flushed estuaries in that it is low in species richness and dominated by estuarine-spawned larvae.

Key words: ichthyoplankton; estuaries; estuary closure; recruitment; seasonality; distribution.

I. INTRODUCTION

Ichthyoplankton assemblages in temperate estuaries typically contain the larvae of many marine teleosts as well as those of species that breed within these systems (e.g. Pearcy & Richards, 1962; Crocker, 1965; Pearcy & Myers, 1974; Able, 1978; Beckley, 1986; Roper, 1986; Johnston & Morse, 1988; Neira *et al.*, 1992). Teleosts that are recruited as larvae into intensively-flushed, macro- and mesotidal estuaries utilize passive and/or selective tidal transport both for movement upstream, often over considerable distances, and for subsequent retention within the estuary (Graham, 1972; Weinstein *et al.*, 1980; Fortier & Leggett, 1982; Norcross & Shaw, 1984; Aprahamian & Barr, 1985; Dando & Demir, 1985; Boehlert & Mundy, 1987, 1988; Laprise & Dodson, 1989, 1990). The larvae of teleosts that are recruited into poorly-flushed, microtidal estuaries (tidal range ≥ 2 m), such as barrier-island and bar-built estuaries, generally enter on flood tides and are then able to remain within these systems by moving either to the bottom and/or the shallow waters along the banks where the seaward flow is considerably reduced (Flores-Coto *et al.*, 1983;

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Beckley, 1985; Roper, 1986; Whitfield, 1989*a*; Lyczkowski-Shultz *et al.*, 1990). The distance to which the larvae of marine teleosts penetrate estuaries depends on the extent of the tidal influence within the system. Thus, in the Severn and Tamar estuaries in the United Kingdom, where the tidal range is large, the larvae of species such as *Dicentrarchus labrax* L. are rapidly transported many kilometres upstream to the salt/freshwater interface (Aprahamian & Barr, 1985; Dando & Demir, 1985), whereas in the Swan Estuary in south-western Australia, where the tidal range in its lower region is less than 1 m, the larvae of marine species rarely penetrate further than 12 km from the estuary mouth (Neira *et al.*, 1992).

The southern coast of Western Australia contains numerous microtidal, bar-built estuaries, such as Wilson Inlet, which are seasonally or temporarily closed to the sea by sand bars across their mouths (Hodgkin & Lenanton, 1981; Lenanton & Hodgkin, 1985). Most of these estuaries have short, narrow entrance channels that open into wide, shallow basins. The narrow mouth and small tidal range characteristic of this region restricts the amount of water that is exchanged between these estuaries and the ocean during each tidal cycle (Hodgkin & di Lollo, 1958; Hodgkin & Clark, 1988). The fact that many of the estuaries in south-western Australia have been subjected to landlocking in the recent past, has been invoked as the main reason why several teleosts, including some typically marine species, are capable of completing their life cycles within these systems (Potter *et al.*, 1986). It is important to recognize, however, that the juveniles and adults of many marine teleosts are also abundant within seasonally closed estuaries such as Wilson Inlet (Potter *et al.*, 1990). Although the larvae of many marine teleosts have been found at the mouth of Wilson Inlet (Neira & Potter, 1992), it is not known whether these larvae enter the basin of this estuary.

In the present study, we describe the seasonal and spatial changes in the composition and abundance of ichthyoplankton within the seasonally closed Wilson Inlet over 20 months, which included two successive periods (spring–early autumn) when most marine and estuarine teleosts spawn in south-western Australia (Thomson, 1957). The data were used to examine whether the ichthyoplankton of this estuary is dominated by the larvae of estuarine species and, if so, to what extent. Particular emphasis was placed on determining whether the species composition of the assemblage of larval fishes within Wilson Inlet changes if the estuary remains open during the whole spawning period of most local marine teleosts, through providing an opportunity for larvae to enter from the sea. Thus, we have compared the larval fish assemblage in Wilson Inlet during the summer and autumn of one year when the estuary was open to the sea (1988/1989) with that of the same period in the preceding year when the estuary was closed (1987/1988). Finally, we have quantified the relative contributions of fish larvae of marine and estuarine species to the assemblage of this estuary, and compared these with those of other estuaries elsewhere in the world in an attempt to relate any differences in the contributions of these two life cycle categories with type of estuary, i.e. poorly *v.* intensively-flushed.

II. MATERIALS AND METHODS

STUDY AREA

Wilson Inlet is a large (area $= 48\ km^2$) and relatively shallow estuary (average depth $< 2{\cdot}0$ m) on the southern coast of temperate Western Australia (Fig. 1). It comprises a large

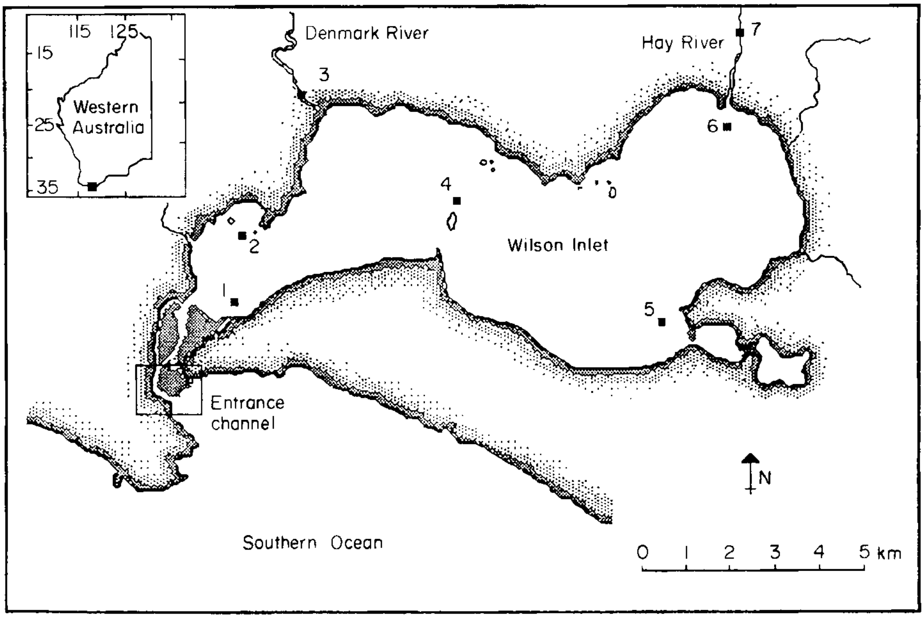

FIG. 1. Location of the sampling sites within the basin (1, 2, 4, 5 and 6) and saline reaches of the tributary rivers (3, 7) of Wilson Inlet in south-western Australia.

basin which is fed by two main tributaries (Denmark and Hay rivers) and opens to the Southern Ocean by a narrow, 1 km long entrance channel (Hodgkin & Clark, 1988). The sand bar which forms at the mouth of the entrance channel during the summer or autumn, and thereby disconnects the estuary from the sea, is artificially breached in the late winter or spring, when the water level within the Denmark River reaches a certain height (Hodgkin & Clark, 1988). During the present study, the estuary mouth was open between 13 October and 19 December 1987 (67 days) and between 13 June 1988 and 15 May 1989 (344 days).

SAMPLING REGIME AND LABORATORY PROCEDURES

Sampling of ichthyoplankton was carried out monthly between September 1987 and April 1989 at sites 1 to 6 in Wilson Inlet (Fig. 1). Site 7 in the Hay River was sampled each month between December 1987 and April 1988 and again between November 1988 and March 1989. For convenience, sites 1, 2, 4, 5 and 6 in the main body of the estuary are termed ' basin sites ', whereas sites 3 and 7 in the saline reaches of the Denmark and Hay Rivers respectively are termed ' riverine sites '.

All sites were sampled at night, commencing approximately 1 h after sunset. Plankton samples were collected using two 0·5 mm mesh conical nets, 0·6 m in diameter and 2·0 m in length, which were attached to either side of a 2·5 m wide, 6 m long power boat. Both nets were towed just below the surface for 10 min at a speed of 1·5 to 2·0 m s^{-1}, following a zig-zag pattern to reduce sampling bias. The volume of water filtered by each net during each tow (range = 110–278 m^3) was obtained using two digital General Oceanic flowmeters. After completing each tow, both nets were washed and the samples fixed in 10% buffered formalin and then preserved in 70% alcohol. The salinity and temperature of the surface waters at each site were measured at the time of sampling, using a portable YEO-KAL Salinity-Conductivity-Temperature meter. Fish eggs were separated into those of the anchovy *Engraulis australis* (Shaw) (see Robertson, 1975) and those belonging to unidentified fishes. The number of eggs of both groups were individually counted except when these exceeded 200, in which case they were estimated by subsampling. Fish larvae were removed from samples using a stereomicroscope, identified to the lowest taxon possible and counted. The term ' larva ' includes the yolk sac, preflexion, flexion and postflexion stages as described by Leis & Trnski (1989). Larvae were identified to family, genus and species level using the larval descriptions given in Uchida *et al.* (1958), Russell (1976), Miller *et al.* (1979), Fahay (1983), Leis & Rennis (1983), Moser *et al.* (1984), Ozawa (1986), Okiyama (1988) and Leis & Trnski (1989). Larvae that could not be identified to at least the family level (including damaged specimens) were placed in the unidentified category (Table I).

LIFE CYCLE CATEGORY DESIGNATIONS

Each species caught as larvae was placed in one of the following four categories: (i) marine straggler (S), i.e. spawns at sea and is rare in estuaries, (ii) marine estuarine-opportunist (O), i.e. spawns at sea and regularly enters estuaries, (iii) estuarine (E), i.e. spawns within estuaries and (iv) fresh water (F), i.e. spawns in rivers (see Lenanton & Potter, 1987). The allocation of each species to one of these categories follows that given in Neira *et al.* (1992), except in the cases of *Favonigobius lateralis* (Macleay) and *Leptatherina presbyteroides* (Richardson), which during the present study have been shown to be capable of breeding within Wilson Inlet as well as in marine waters.

TREATMENT OF DATA

The total number of eggs of unidentified teleosts and of *E. australis*, and the total number of larvae and those of each species caught in both nets at each site in each month were each summed and converted to a concentration, i.e. numbers per 100 m^3. Mean monthly values given for the concentration of fish eggs, larvae and the number of species in Fig. 2, and for the numbers of larvae of the various species in each month in Fig. 3 (= sum of the concentrations at each site), utilized data for all seven sites. The total numbers of fish eggs and larvae and the mean values for the number of species at each site in Fig. 4 and the total number of larvae of the various species in Fig. 5 are restricted to data collected for 5 months when the estuary was open to the sea (= sum of the concentrations of each month between December 1988 and April 1989) and for the same period in the preceding year when it was closed to the sea (= sum of the concentrations of each month between December 1987 and April 1988). The percentage contributions of fish eggs and the larvae of the different species in the whole system and at the different sites (Table I) and, in the case of the larvae, also to the different life cycle categories (Table II), were calculated from the mean concentrations for each month of the year, after the values for the months between September and April in both 1987/1988 and 1988/1989 had each been averaged to obtain a single value for those months.

Classification and Multi-Dimensional Scaling (MDS) analyses were undertaken using the Pattern Analysis Package (PATN) of Belbin (1987). The analyses, which employed the mean concentrations of that species which contributed $\geq 0{\cdot}1\%$ to the total catch (Table I), were used to examine the degree of similarity between sites during the periods when the estuary was closed (December 1987–April 1988) and open to the sea (December 1988–April 1989). A two-dimensional matrix was constructed from the original species × site × time data set, which contained the mean concentrations of each species (11) at each of the seven sites during the period when the estuary was closed and when it was open (14). Values in the matrix were standardized using the range standardization option of PATN before it was transformed into an association matrix using the Bray–Curtis measure of dissimilarity. The resultant association matrix was then employed for classification and MDS, using flexible unweighted pair group arithmetic averaging (UPGMA, $\beta = -0{\cdot}1$) to construct the dendrogram (Belbin, 1987). A Bray–Curtis percent value of 100 means complete dissimilarity and a value of 0 complete similarity.

III. RESULTS

ENVIRONMENTAL CONDITIONS

The mean surface salinity within Wilson Inlet underwent marked seasonal changes (Fig. 2), which reflected the hydrological effects of the closing and opening of the estuary mouth, as well as seasonal rainfall patterns. Salinity increased from 18·7‰ in September 1987 to 22·0‰ in December, before rising to 28·4‰ in April 1988 as a result of evaporation during this dry period when the estuary was closed

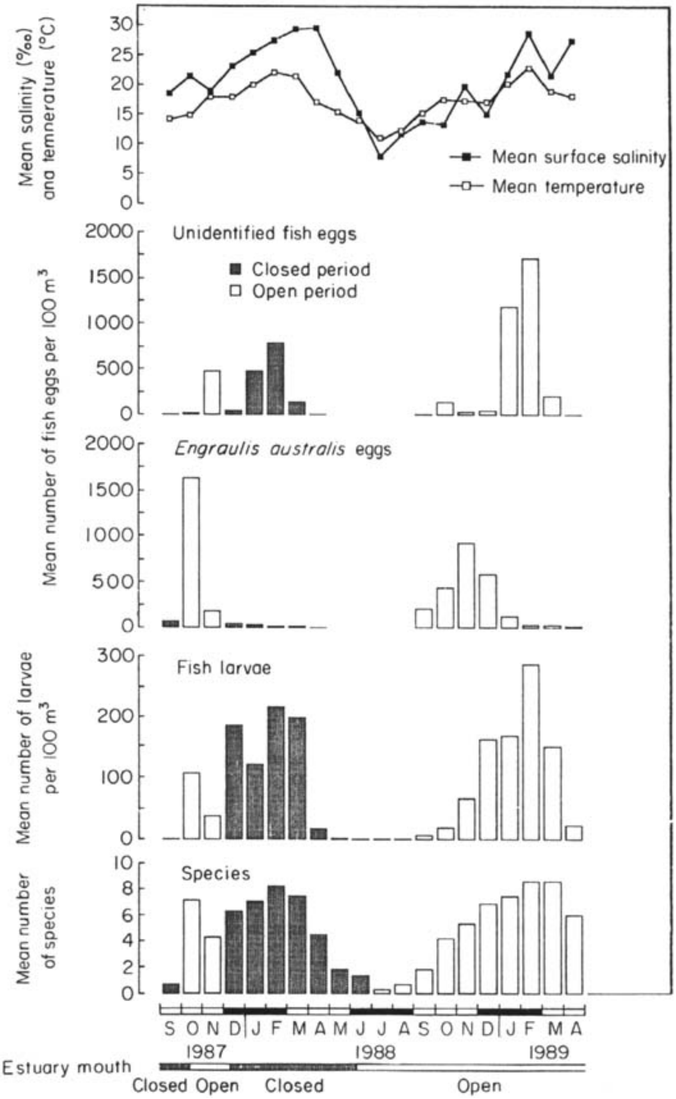

FIG. 2. Mean surface salinities and temperatures, the mean concentrations (number per 100 m³) of fish eggs and fish larvae and the mean number of species in Wilson Inlet in each month between September 1987 and April 1989. Means were calculated from data collected for all seven sampling sites. Open and black boxes on the horizontal axis represent spring and autumn months and the summer and winter months, respectively. Stippled and open boxes below the horizontal axis represent the periods in which the estuary was closed and open to the sea, respectively.

to the sea. The heavy rainfall, which started in May 1988, resulted in the salinity declining to a minimum of 7·9‰ in July. Although the sand bar was breached in June 1988, the influx of marine water into the basin of Wilson Inlet was so gradual that it did not produce a change in surface salinity until August, and even then it rose only to 11·5‰. Salinity gradually increased during the following months, reaching a maximum of 28·7‰ in February 1989 (Fig. 2).

Mean water temperatures throughout the estuary followed a similar seasonal pattern to that of surface salinity. Temperature increased from 14·9° C in

September 1987 to 22·3° C in February 1988 and then declined to a minimum of 10·9° C in July, before rising again to reach a maximum of 22·9° C in February 1989 (Fig. 2).

COMPOSITION OF ICHTHYOPLANKTON

A total of 221 102 fish eggs and 39 068 fish larvae were collected from the five basin and two riverine sites in Wilson Inlet between September 1987 and April 1989. Of all fish eggs, 43·7% belonged to *E. australis* and the remainder to unidentified fishes. The larval fish assemblage comprised 25 species belonging to 17 families. Only three larvae could not be identified to at least family level (Table I). The most abundant family was the Gobiidae, comprising 56·9% of the total catch, followed by the Engraulididae (27·9%), Blenniidae (10·1%) and Syngnathidae (3·9%). The Atherinidae, Hemiramphidae, Clinidae and Platycephalidae collectively contributed 1·3% and the remaining nine families were rare (Table I). The most abundant species were *Pseudogobius olorum* (Sauvage) and *E. australis*, accounting for 43·9 and 27·9% of the total number of larvae caught, respectively (Table I). The four other relatively abundant species were *Parablennius tasmanianus* (Richardson) (10·1%), *Favonigobius suppositus* (Sauvage) (9·2%), *Urocampus carinirostris* (Castelnau) (3·9%) and *Favonigobius lateralis* (Macleay) (3·7%).

SEASONAL CHANGES IN ICHTHYOPLANKTON ABUNDANCE

Mean concentrations of fish eggs and larvae and the mean number of species in Wilson Inlet followed similar seasonal trends (Fig. 2). Mean concentrations of unidentified fish eggs peaked in February in both 1988 and 1989, with values of 785 and 1713 eggs per 100 m^3, respectively. Mean concentrations of *E. australis* eggs peaked in October 1987 and November 1988, with values of 1626 and 920 eggs per 100 m^3, respectively. No eggs were found between May and August (Fig. 2).

Mean concentrations of fish larvae were high between December and March and peaked in February 1988 and 1989, with values of 216 and 286 larvae per 100 m^3, respectively. Few fish larvae were caught between May and September (Fig. 2).

The mean number of species was greatest between mid-spring and mid-autumn and was very low during winter. The maximum monthly mean number of species (8) was recorded in February 1988 and in February and March 1989 (Fig. 2).

The larvae of the six most common species were abundant between mid-spring and early autumn (October to March) and were rare or absent between late autumn and early spring (Fig. 3). The numbers of *F. lateralis*, *P. tasmanianus* and *P. olorum* each reached a maximum between December and March, with the peak for each species being attained at a similar time in 1987/1988 and 1988/1989. Large numbers of larval *E. australis* and *U. carinirostris* were caught in October 1987 and from December to May. Larvae of *F. suppositus* were caught between October and April, with numbers being considerably greater in November and December 1988 than in the same months in 1987. The larvae of all of the above species were caught over a protracted period, with those of *P. olorum* being recorded in every month except August 1988 (Fig. 3).

SPATIAL DISTRIBUTION OF ICHTHYOPLANKTON

During this study, over 88% of the unidentified fish eggs were collected at sites 1 and 2 at the lower end of the estuary, and 87% of those of *E. australis* were obtained from sites 1, 2 and 4 (Table I). Only 6·5% of all fish eggs came from sites 3 and 7 in the rivers (Table I). The number of unidentified fish eggs collected at sites 1 and 2 in the basin was approximately four and two times greater when the estuary was open to the sea than when it was closed. Similarly, the eggs of *E. australis* at sites 1, 2 and 4 in the basin were far more abundant during the open period (Fig. 4).

Over 59% of all fish larvae were caught at sites 1, 2, 4 and 5, with almost 20% being collected at Site 2, 4·1 km from the estuary mouth (Table I). The total number of fish larvae collected at sites 1, 4, 5 and 6 and at Site 7 were greater when the estuary was open to the sea than when it was closed, whereas the reverse situation occurred at Site 2 in the basin and at Site 3 in the Denmark River (Fig. 4). The large number of fish larvae caught during the closed period at Site 3 was mainly due to the large catch of the gobiid *P. olorum* at that time (Fig. 5).

The mean number of species recorded at each site during the present study was low and varied from three at Site 7, in the upper end of the estuary, to eight at Site 2, 4·1 km from the estuary mouth. The mean number of species recorded at each site during the closed period was generally similar to that during the open period, with values ranging from four to seven and from five to eight, respectively (Fig. 4).

More than 85% of the larvae of *E. australis*, *U. carinirostris* and *F. lateralis* caught during this study came from sites 1, 2, 4 and 5 in the basin (Table I). The number of larvae of these three species in both closed and open periods were in general lowest at Site 6 at the upper end of the basin and at the two riverine sites (Fig. 5). In contrast, the larvae of *P. tasmanianus*, *P. olorum* and *F. suppositus* were more abundant at either one or both riverine sites than at the basin sites. The larvae of *E. australis* at each of the sites were invariably more abundant during the open period, particularly at sites 4 and 5 in the basin, where the numbers caught were approximately four times those collected at those sites when the estuary was closed (Fig. 5). The larvae of *P. tasmanianus* and *P. olorum* at sites 3 and 7 in the rivers were more abundant during the closed than the open period, whereas the reverse situation pertained with the larvae of *F. suppositus* (Fig. 5).

CONTRIBUTION OF LIFE CYCLE CATEGORIES

The larval fish assemblage of Wilson Inlet was dominated by the larvae of teleosts that spawn within the estuary, both in terms of number of species (64%) and contribution to the total catch (99·9%). All of the 16 estuarine-spawning species were recorded in the rivers and, of these, all except *Leptatherina wallacei* (Prince, Ivantsoff & Potter), *Acanthopagrus butcheri* (Munro) and an unidentified terapontid, were found in the basin (Tables I, II).

Although the larvae of six species of marine straggler, two species of marine estuarine-opportunist and one freshwater species were caught, their numbers were very low (Tables I, II). The larvae of the marine stragglers, which were found predominantly at Site 1, were all collected in December 1988, when the estuary was open to the sea.

CLASSIFICATION OF THE LARVAL FISH ASSEMBLAGE DURING CLOSED AND OPEN PERIODS

Classification of sites, using the species concentrations in the assemblage sampled during the closed (December 1987–April 1988) and open periods (December 1988–April 1989) separated sites 1, 2, 4 and 5 in the basin from sites 3

TABLE I. Rank by abundance of families and species of fishes collected as larvae between September 1987 and April 1989 from five basin and two riverine sites within Wilson Inlet

Rank	Family Species	(Rank species No)	Total Contribution Family (%)	Total Contribution Species (%)	Contribution per site (%) Basin 1	Basin 2	Basin 4	Basin 5	Basin 6	Rivers 3	Rivers 7	Total	Life cycle category
1	Gobiidae		3431 (56·9)										
	Pseudogobius olorum (Sauvage)	(1)		2650 (43·9)	31·4	42·4	22·4	39·7	37·3	69·7	28·1	16 926	E
	Favonigobius suppositus (Sauvage)	(4)		553 (9·2)	1·1	0·7	0·5	2·6	4·6	9·6	65·9	2915	E
	Favonigobius lateralis (Macleay)	(6)		225 (3·7)	8·6	5·2	3·6	4·0	3·7	1·1	0·8	1496	E
	Gobiid 1	(13)		2	<0·1	0·1	<0·1	<0·1	0·2	<0·1		14	E
2	Engraulididae		1685 (27·9)										
	Engraulis australis (Shaw)	(2)		1685 (27·9)	43·0	33·3	63·5	39·3	16·7	3·9	3·8	11 792	E
3	Blenniidae		601 (10·1)										
	Parablennius tasmanianus (Richardson)	(3)		601 (10·1)	5·9	12·9	5·0	4·8	27·1	14·4	1·1	600	E
4	Syngnathidae		235 (3·9)										
	Urocampus carinirostris Castelnau	(5)		235 (3·9)	8·6	4·3	3·9	7·4	4·8	0·6	<0·1	1617	E
5	Atherinidae		36 (0·6)										
	Atherinosoma elongata Klunzinger	(8)		21 (0·3)	0·5	0·1	0·1	1·0	1·0	0·3		132	E
	Leptatherina presbyteroides Richardson	(9)		14 (0·2)	0·3	0·2	0·1	0·1	0·9	0·3		88	E
	Leptatherina wallacei Prince, Ivantsoff & Potter	(14)		1							0·2	7	E
6	Hemiramphidae		24 (0·4)										
	Hyporhamphus melanochir (Valenciennes)	(7)		24 (0·4)	<0·1	0·3	0·5	0·8	3·1	<0·1		163	E
7	Clinidae		10 (0·2)										
	Cristiceps australis Valenciennes	(10)		9 (0·2)	0·3	0·4	0·2	<0·1	0·3	<0·1		60	E
	Ophiclinus gracilis Waite	(19)		0·5	0·1							2	S

8	Platycephalidae		6 (0·1)										
	Platycephalus speculator Klunzinger	(11)		6 (0·1)	<0·1	0·1	0·2	0·2	0·1	<0·1		41	E
9	Galaxiidae		1										
	Galaxias occidentalis Ogilby	(14)		1					0·2	<0·1		4	F
	Labridae		1										
	Labrid Julidini	(14)		1	0·1							3	S
	Pictilabrus sp.	(19)		<0·5	<0·1							1	S
	Labrid 2	(19)		<0·5	<0·1							1	S
	Plotosidae		1										
	Cnidoglanis macrocephalus (Valenciennes)	(14)		1	0·1	<0·1						7	E
12	Terapontidae		<0·5										
	Terapontid 1	(19)		<0·5							0·1	2	E
	Sillaginidae		<0·5										
	Sillaginodes punctata (Cuvier)	(19)		<0·5					0·1			1	O
	Clupeidae		<0·5										
	Hyperlophus vittatus (Castelnau)	(19)	<0·5	<0·5						<0·1		1	O
	Cynoglossidae												
	Cynoglossus broadhursti Waite	(19)		<0·5				<0·1				1	S
	Sparidae		<0·5										
	Acanthopagrus butcheri (Munro)	(19)		<0·5							<0·1	1	E
	Crediidae		<0·5										
	Limnichthys fasciata Waite	(19)		<0·5	<0·1							1	S
	Unidentified	(19)		<0·5		<0·1				<0·1		3	
	Total		6031		815	1172	772	812	300	1644	516	39 068	
	(%)				(13·5)	(19·4)	(12·8)	(13·5)	(5·0)	(27·2)	(8·6)		
	Eggs												
	Unidentified fish eggs			17 536 (56·3)	69·5	66·9	16·5	29·9	27·2	41·9	81·1	129 410	
	Engraulis australis			13 610 (43·7)	30·5	33·1	83·5	70·1	72·8	58·1	18·9	91 692	
	Total			31 146	8252	13 908	5695	1286	68	1084	853	221 102	
	(%)				(26·5)	(44·7)	(18·3)	(4·1)	(0·2)	(3·5)	(2·7)		

The total numbers of the eggs of unidentified fishes and of *Engraulis australis* and their percentage contributions at the different sites are also given. Except for the values given for the total number of eggs and larvae, the rank and all other values have been calculated from the concentrations (numbers per 100 m^3) at each site after these were averaged for a period of 12 months (see Materials and Methods for further details). n.b. Percentages for the contribution of each family and species to the total larval fish assemblage are given only when they exceed 0·1%. E, Estuarine; F, freshwater; O, marine estuarine–opportunist; S, marine straggler.

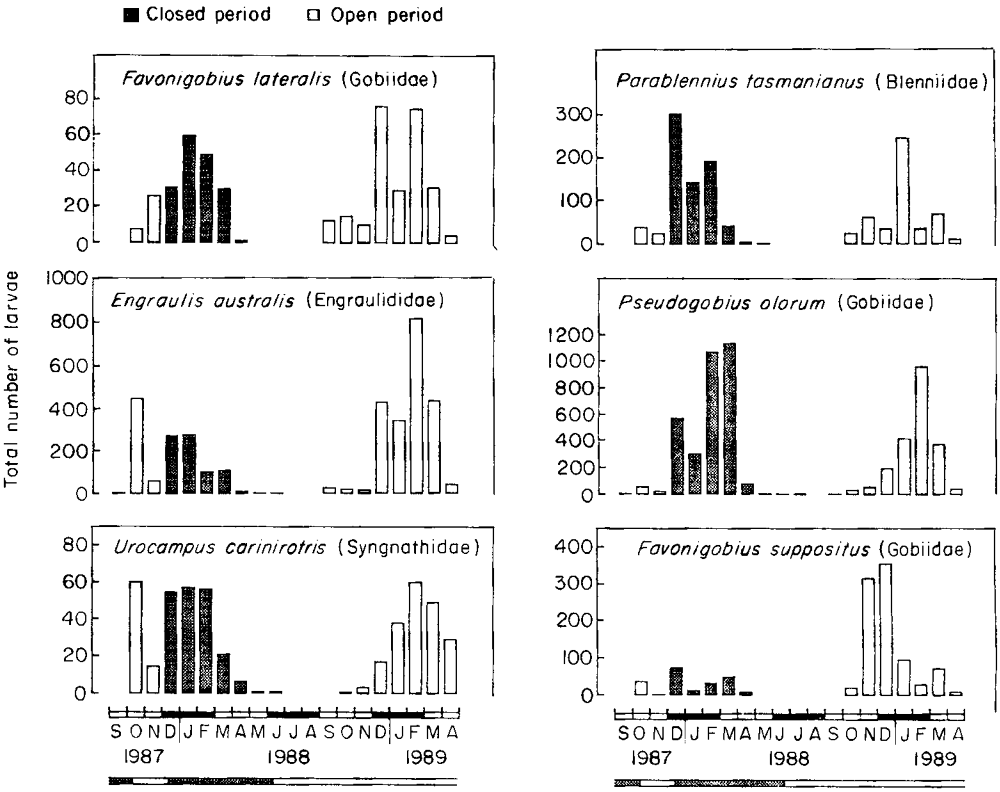

FIG. 3. Total number of the larvae of the six most abundant teleost species collected in Wilson Inlet in each month between September 1987 and April 1989. Each monthly value represents the sum of the numbers caught at seven sites after they had been adjusted to 100 m^3. Open and black boxes on the horizontal axis represent spring and autumn months and the summer and winter months, respectively. Stippled and open boxes below the horizontal axis represent the periods in which the estuary was closed and open to the sea, respectively.

and 7 in the rivers at the 50% dissimilarity level, irrespective of whether the estuary was closed or open to the sea (Fig. 6). Site 6, immediately opposite the Hay River at the upper end of the basin (Fig. 1), grouped with the basin sites in the period when the estuary was open and with the riverine sites in the period when it was closed. The sites within the basin grouped according to distance from estuary mouth. Thus, for example, Site 1 in the closed and open periods grouped together, and the same was true for Site 2, with Sites 4 and 5 further up the basin successively clustering with those from near the estuary mouth. Within the riverine group, Site 3 in the open and closed period grouped together, as also did Site 7. The MDS ordination provided a similar result to classification, with all the basin sites grouping separately from the riverine sites, except in the case of Site 6 in the closed period (Fig. 6).

IV. DISCUSSION

CONTRIBUTION AND SEASONALITY OF ESTUARINE-SPAWNED LARVAE

The larvae of species that spawn within Wilson Inlet dominated the ichthyoplankton assemblage of this estuary during the present 20-month study,

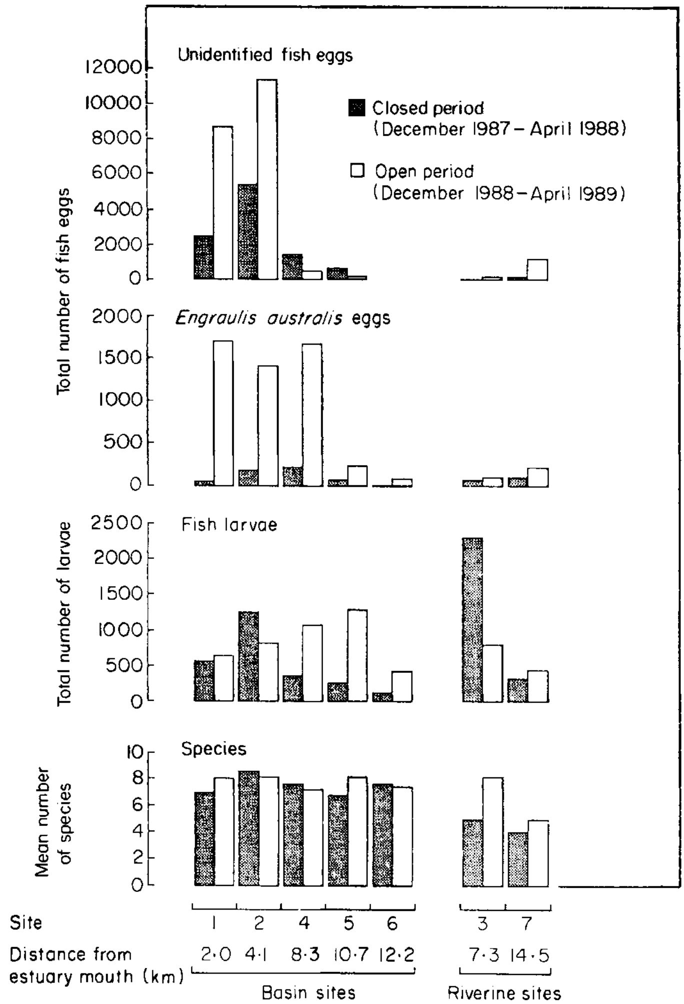

FIG. 4. Total numbers of fish eggs and fish larvae and the mean number of species recorded in Wilson Inlet at each of the seven sampling sites during the 5 months when the estuary was closed (December 1987 April 1988) and open to the sea (December 1988–April 1989). Numbers represent the sum of the numbers of larvae caught in all 5 months in each period after they had been adjusted to 100 m³. The distance (km) from the estuary mouth to each of the sites in the basin and the two tributary rivers is also given.

accounting for 64% of the number of species and 99·9% of the total number of larvae. The larvae of estuarine-spawning species also dominate the larval assemblage of the permanently open Swan Estuary in south-western Australia (Neira *et al.*, 1992), as well as other poorly-flushed estuaries such as the Swartkops (permanently open) and Swartvlei (seasonally closed) estuaries in southern Africa (Melville-Smith & Baird, 1980; Whitfield, 1989*b*) and the Tamiahua Lagoon (permanently open) in Mexico (Flores-Coto *et al.*, 1983).

The dominance of estuarine-spawned larvae in both Wilson Inlet and the Swan Estuary reflects the very high collective contributions of estuarine-spawning populations of the Gobiidae and of *E. australis* in Wilson Inlet (84·8%) and of the

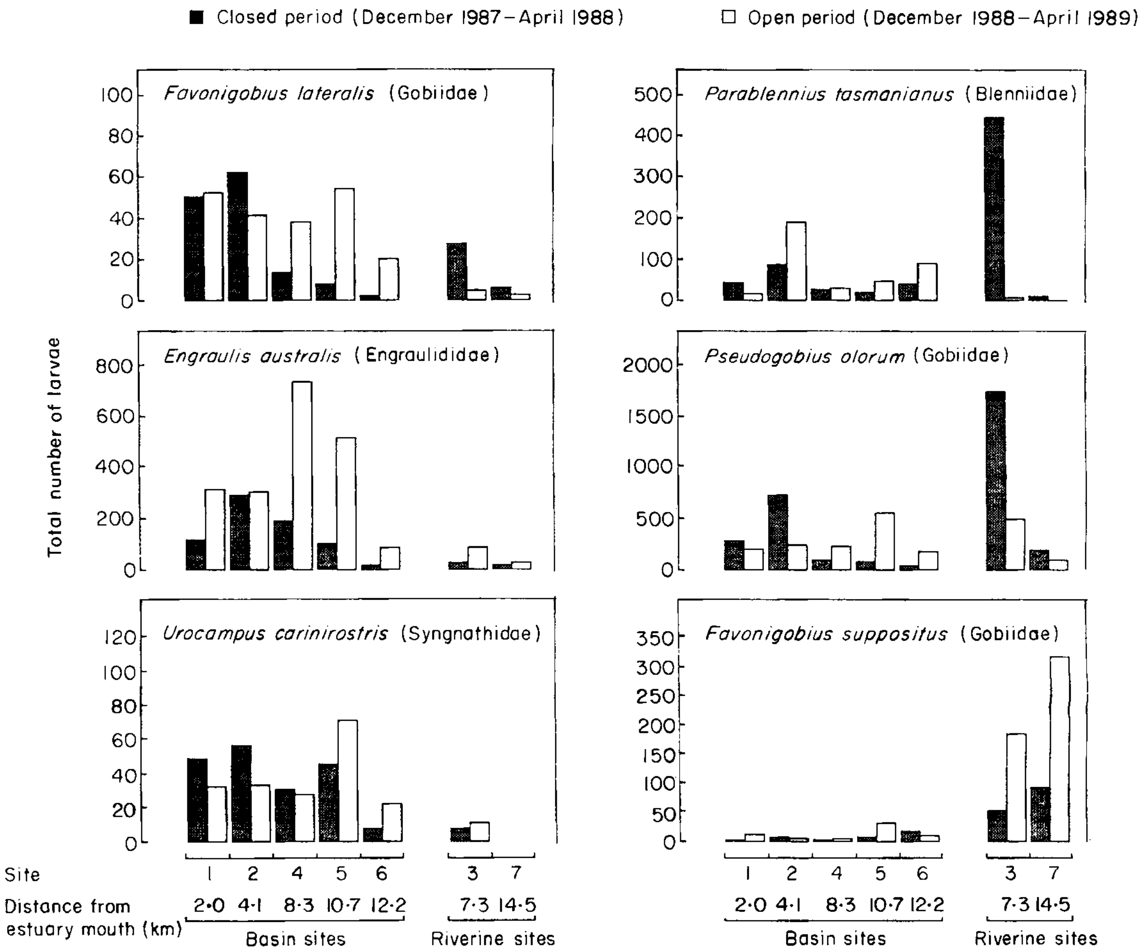

FIG. 5. Total numbers of the larvae of the six most abundant teleost species collected in Wilson Inlet at each of the seven sampling sites during the 5 months when the estuary was closed (December 1987–April 1988) and open to the sea (December 1988–April 1989). Numbers represent the sum of the numbers of larvae caught in all 5 months in each period after they had been adjusted to 100 m^3. The distance (km) from the estuary mouth to each of the sites in the basin and the two tributary rivers is also given.

Gobiidae in the Swan Estuary (88·2%) (Neira *et al.*, 1992). Similarities between the larval composition of these two estuaries is further emphasized by the fact that, in both estuaries, *P. olorum* was the dominant species. The Gobiidae makes a major contribution to larval fish assemblages in estuaries and protected inshore-marine embayments in temperate regions elsewhere in the world (e.g. Pearcy & Myers, 1974; Melville-Smith & Baird, 1980; Miller, 1984; Steffe & Pease, 1988; Drake & Arias, 1991), and *E. australis* is known to spawn within various estuaries in temperate Australia (Blackburn, 1950; Arnott & McKinnon, 1985; Neira *et al.*, 1992).

The periods when the number of species and the abundance of individual species in Wilson Inlet peaked in both 1987/1988 and 1988/1989, i.e. mid spring–early autumn, are consistent with the time of year when most estuarine-spawning teleosts typically breed in south-western Australia (Thomson, 1957). This period

TABLE II. Number of species and number of larvae of marine stragglers, marine estuarine-opportunists, estuarine and freshwater species, and the percentage contribution of each to the totals recorded for the whole Wilson Inlet and for the sites in the basin (5) and rivers (2)

Life cycle category	Whole system		Basin sites		Riverine sites	
	n	(%)	*n*	(%)	*n*	(%)
No. of species:						
Stragglers	6	(24·0)	6	(31·8)	0	(0·0)
Estuarine-opportunists	2	(8·0)	1	(4·5)	1	(5·5)
Estuarine	16	(64·0)	13	(59·1)	16	(88·9)
Freshwater	1	(4·0)	1	(4·5)	1	(5·5)
Total	25		21		18	
No. of larvae:						
Stragglers	2	(<0·1)	2	(0·1)	0	(0·0)
Estuarine-opportunists		(<0·1)		(<0·1)		(<0·1)
Estuarine	6027	(99·9)	3868	(99·9)	2159	(100·0)
Freshwater	2	(<0·1)	1	(<0·1)	1	(<0·1)
Total	6031		3871		2160	

also corresponds to that when teleosts spawn in estuaries and inshore-marine embayments elsewhere in temperate Australia (e.g. Jenkins, 1986; Steffe & Pease, 1988; Gaughan *et al.*, 1990; Neira *et al.*, 1992) and in other regions of the world (e.g. Pearcy & Richards, 1962; Chenoweth, 1973; Pearcy & Myers, 1974; Misitano, 1977; Melville-Smith & Baird, 1980; Florest-Coto *et al.*, 1983; Beckley, 1986; Roper, 1986; Whitfield, 1989*b*; Drake & Arias, 1991). Although the overall abundance of larvae in Wilson Inlet peaked approximately 2 months later than in the Swan Estuary (i.e. February/March *v.* December/January) (Neira *et al.*, 1992), the water temperatures at the time of peak abundance in both systems were 19–21° C. The later peak in Wilson Inlet may thus in part be related to a relatively later attainment of these water temperatures in this more southern and therefore cooler estuary.

RARITY OF MARINE-SPAWNED LARVAE

The present study demonstrated that the larvae of marine teleosts are rarely recruited into the basin of Wilson Inlet, even though in the second year the estuary remained open throughout the main period when such species spawn at sea. Indeed, only eight of the 25 species caught as larvae within the estuary belonged to marine species and these collectively contributed only 0·03% to the total catch. Larvae of marine teleosts are also rare in other poorly-flushed estuaries such as those found in southern Africa (e.g. Melville-Smith & Baird, 1980; Whitfield, 1989*a*) and Mexico (e.g. Flores-Coto *et al.*, 1983). The virtual absence of marine-spawned larvae within the basin of Wilson Inlet can be related to the restricted movement of tidal marine water within this part of the system during each tidal cycle (Hodgkin & Clark, 1988), which results from the combination of the small tidal range in south-western Australia (Spencer, 1956) and the narrowness and

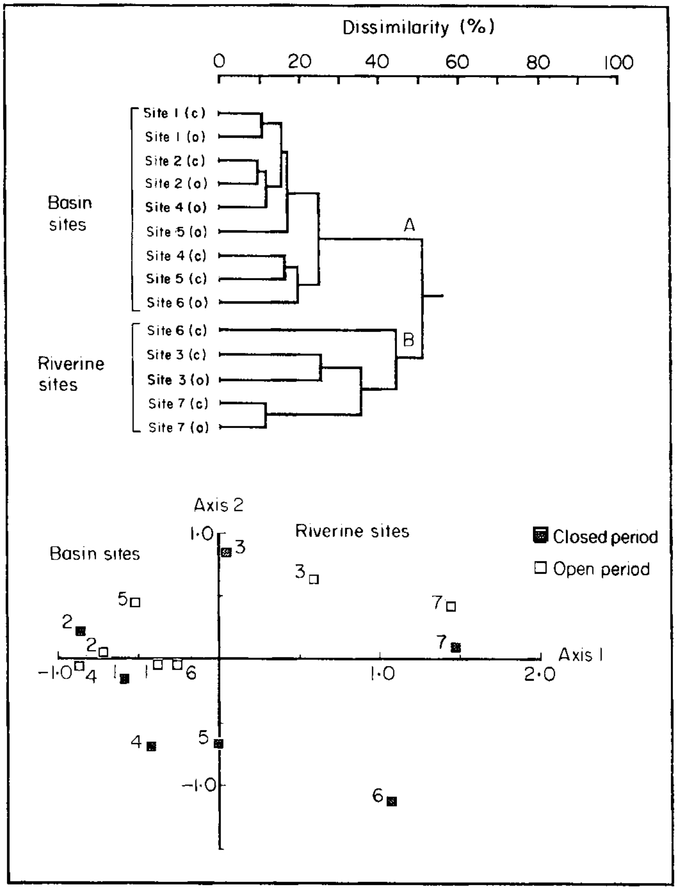

FIG. 6. Classification and MDS ordination of the samples collected from the five sites in the basin (1, 2, 4, 5 and 6) and two sites in the rivers (3 and 7) in Wilson Inlet during the 5 months when the estuary was closed (December 1987–April 1988) and open to the sea (December 1988–April 1989).

shallowness of the entrance channel of this estuary. This means that the tidal current, often available for movement and/or dispersion of marine-spawned larvae within intensively-flushed estuaries, is essentially absent in the very poorly-flushed Wilson Inlet. However, while well-developed larvae (i.e. postflexion) of a few marine species have been collected within the entrance channel of Wilson Inlet (Neira & Potter, 1992), they were not found in the basin of Wilson Inlet during the present study. They may thus settle in the bottom or along the banks where the seaward flow is minimum, a situation that would parallel the way in which well-developed larvae of some marine species enter Lake Macquarie in eastern Australia (Miskiewicz, 1986), the Swartkops and Swartvlei estuaries in southern Africa (Beckley, 1985; Whitfield, 1989*a*) and Whangateau Harbour in New Zealand (Roper, 1986).

The paucity of the larvae of marine teleosts caught within Wilson Inlet implies that the teleosts which utilize this system as a nursery area are typically recruited during their juvenile rather than larval phase. Such a situation would parallel that found in other south-western Australian estuaries, e.g. the Blackwood and Swan estuaries, where abundant teleosts such as *Rhabdosargus sarba* (Forsskål), *Mugil cephalus* Linnaeus, *Aldrichetta forsteri* (Valenciennes) and *Torquigener pleurogramma* (Regan), have been shown to be recruited as juveniles (cf. Lenanton, 1977; Chubb *et al.*, 1981; Potter *et al.*, 1988).

The number of marine species collected as larvae during a concomitant study in the entrance channel of Wilson Inlet during December and January (Neira & Potter, 1992) is similar to that recorded by Neira *et al.* (1992) in the entrance channel (lower estuary) of the Swan Estuary, i.e. 51 and 59 species respectively. However, despite the fact that the distance from the mouth of the estuary to the most seaward sampling site in the basin was much less in Wilson Inlet than in the Swan Estuary (2·0 *v.* 9·0 km), the number of marine species that were caught at those sites was greater in the latter system (i.e. 8 *v.* 32) (cf. results of the present study and Neira *et al.*, 1992). The tendency for the larvae of marine species to penetrate further into the Swan Estuary than into Wilson Inlet presumably reflects the greater exchange of water that occurs between the lower reaches of this estuary and the sea as a result of its deeper (5–16 *v.* 1·5 m max.) and wider (400–600 *v.* 50 m max.) entrance channel. It should be noted, however, that the Swan Estuary is still not a well-flushed estuary, as indicated by the fact that the total number of marine-spawned larvae found at the upper end of the basin was still small, contributing only 6·2% of the total catch in that region (Neira *et al.*, 1992).

ABUNDANCE AND DISTRIBUTION OF FISH EGGS AND LARVAE DURING CLOSED AND OPEN PERIODS

The overall abundance of *E. australis* eggs was greatest during months when the estuary was open to the sea (October and November 1987 and September 1988 to December 1989), which corresponds to the time when this species spawns in other south-western Australian estuaries, i.e. spring (Neira *et al.*, 1992; F. J. Neira, unpublished). Since *E. australis* spawns mainly when salinities exceed 15·8‰ (Arnott & McKinnon, 1985), the higher peak in egg abundance in October 1987 than in November 1988 (1620 *v.* 920 eggs per 100 m^3), as well as the more protracted spawning in 1988, is probably related to the different salinity regimes at those times. Thus, the relatively dry winter and spring of 1987 resulted in mean salinities reaching 21‰ by October, a feature which could have accounted for the sharp peak in egg abundance in that month. In contrast, the greater rainfall in the winter and spring of 1988 than in 1987 resulted in mean salinities reaching only 17·9‰ by November 1988, a feature which could account for the peak in egg abundance being delayed until that month and being not as marked as in the previous year. The fact that eggs of *E. australis* during the period when the estuary was open to the sea were most abundant at sites near the estuary mouth (2·0–8·3 km from estuary mouth), also emphasizes that spawning takes place mainly in regions of higher salinities. It should be noted, however, that the overall greater abundance of eggs during the open period (December 1988–April 1989) than in the closed period (December 1987–April 1988) reflects the delayed and more protracted spawning period of this species in 1988. Since *E. australis* exhibit peak egg production in the spring and the mouth of Wilson Inlet closes generally in summer or autumn, the closure of the estuary is unlikely to have an effect in the spawning success of this species in this system.

Although it was not possible to identify most of the pelagic eggs of other teleosts (termed ‘ unidentified fish eggs ’ throughout the text), some eggs at a late stage (i.e. with embryos) were identified as those of *Platycephalus speculator* Klunzinger, a species that spawns within the estuary (Hyndes *et al.*, 1992). In contrast to the situation with the eggs of *E. australis*, those of unidentified teleosts peaked in the same month in both years. Since this peak was reached in February, it occurred after the estuary mouth had closed in the summer of 1987/1988, but while it was still open in the following year. It is also worth noting that the trends shown by the mean overall abundance of larvae, most of which hatched from demersal eggs, was similar in the 2 years.

Classification and MDS ordination showed that the composition of the larval fish fauna in the basin differed from those in the saline regions of the rivers, reflecting the greater contribution of species such as *E. australis*, *F. lateralis* and *U. carinirostris* in the basin and of *P. olorum* and *F. suppositus* in the rivers. The paucity of the larvae of *P. olorum* and *F. suppositus* in the basin contrasts with the large numbers of their juveniles and adults in that part of the system (I. C. Potter *et al.*, unpublished). This implies that adults of these two gobiids move into the saline reaches of rivers to spawn.

The results of classification and MDS ordination also demonstrated that the composition of the larval fish fauna at any given site in the period when the estuary was closed to the sea (December 1987–April 1988) was similar to that of the corresponding site during the period when the estuary was open (December 1988–April 1989). These similarities reflect the fact that (1) the larval fish fauna of Wilson Inlet was dominated by the same estuarine species in both periods, (2) each of the more abundant species almost invariably exhibited similar patterns of spatial distribution and reached peak abundance at a similar time in both periods, and (3) the larvae of marine species were very rare, even in 1988/1989 when the estuary remained connected to the sea for several months, thereby providing an opportunity for marine-spawned larvae to enter from the sea.

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