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The Larval Fish Assemblage of the Nornalup–Walpole Estuary, a Permanently Open Estuary on the Southern Coast of Western Australia

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Abstract

Fish larvae were sampled in the entrance channel and in the two basins of the permanently open Nornalup–Walpole Estuary, on the southern coast of Western Australia, in each month between October 1989 and September 1990. Sampling yielded a total of 39 068 larvae belonging to 36 species and 23 families, with the engraulidid *Engraulis australis* (56·7%) and the gobies *Pseudogobius olorum* (24·4%) and *Favonigobius lateralis* (15·0%) being the most abundant species. Most of the larvae were caught between November and March, with the concentrations of the most abundant species reaching peaks between January and March, when water temperatures had reached 21–24°C. In terms of number of larvae, the larval fish assemblage in the basins was dominated by species that spawn within the estuary, with the larvae of these species contributing ≥98·7% to the totals at the basin sites. Although the larvae of 26 marine species were caught in the entrance channel, these were either rare or absent in the basins, except for those of the terapontid *Pelates sexlineatus*, which were moderately abundant in the outer basin. The fact that the larvae of most of these marine species were at the preflexion stage, and that all but three of those species had never been previously recorded as either juveniles or adults within the system, indicates that they were passively transported from outside the estuary. The absence of larvae of most of the marine teleosts that are abundant in the basins of the Nornalup–Walpole Estuary parallels the situation in the nearby and seasonally closed Wilson Inlet.

Introduction

Estuaries are used as nursery areas by a wide range of marine teleosts (Haedrich 1983; Kennish 1990; Potter *et al.* 1990). Some of these species enter large, well flushed estuaries in the Northern Hemisphere as larvae, using passive and/or selective tidal transport both for entry into and retention within these systems (e.g. Weinstein *et al.* 1980; Fortier and Leggett 1982; Boehlert and Mundy 1988). In contrast, in poorly-flushed estuaries in the temperate regions of Africa, Australia and New Zealand, where for much of the year the two-layered circulation pattern is less pronounced, the larvae of some marine species enter these systems on the flood tides and are retained by rapidly settling along the banks or on the bottom, where water movements are reduced (Beckley 1985; Roper 1986; Whitfield 1989*a*).

Two recent studies on larval fishes in Wilson Inlet, a seasonally closed estuary on the southern coast of Western Australia, showed that, although the larvae of 51 marine fish species were caught in the entrance channel, the larvae of only seven of these species were collected in the large basin of that system and then only in very small numbers (cf. Neira and Potter 1992*a*, 1992*b*). The paucity of marine-spawned larvae in Wilson Inlet was attributed to the restricted tidal exchange that occurs through the narrow and shallow entrance channel of that system (Neira and Potter 1992*b*) and to the fact that, in one of the two years of the study, the estuary was closed in summer, i.e. in the period when several marine fish species spawn in south-western Australia (Thomson 1957).

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The juvenile and adult fish faunas in the shallows of the permanently open Nornalup–Walpole Estuary, and also in the seasonally closed Wilson Inlet, approximately 70 km further east, are dominated by estuarine species (Potter *et al.* 1993; Potter and Hyndes 1994). However, the prevalence of juveniles and adults of marine species in deeper waters is greater in the Nornalup–Walpole Estuary than in Wilson Inlet, presumably reflecting the presence of a permanently open, short and deeper entrance channel, a greater tidal exchange with the sea and higher salinities. The present study was therefore undertaken to determine the composition of the larval assemblage of the Nornalup–Walpole Estuary and to ascertain whether the marine species that are abundant in this estuary are recruited as larvae. This paper describes both the composition of the larval fish assemblage and the way in which the concentrations of the main species vary seasonally and with location in the estuary. The results are compared with those obtained during a parallel study of the juvenile and adult fish fauna of the Nornalup–Walpole Estuary (Potter and Hyndes 1994) and with those obtained in two studies on larval fishes in the nearby Wilson Inlet (Neira and Potter 1992*a*, 1992*b*).

Materials and Methods

Sampling Locality and Regime

The Nornalup–Walpole Estuary, a permanently open system on the southern coast of Western Australia, comprises the Nornalup and Walpole Inlets, which are joined by a 1-km-long channel (Fig. 1). The system has a total area of 13 km^2 and an average depth of 4 m in the large Nornalup Inlet and 2 m in the smaller Walpole Inlet. The Nornalup Inlet opens to a moderately strong surf zone in the Southern Ocean by a short (~160 m), narrow channel approximately 2–5 m deep. The estuary is always tidal (tidal range <1·0 m), and the combination of tidal exchange and river flow keeps the sand bar open all year (Hodgkin and Clark, 1988).

Fish larvae were sampled monthly between October 1989 and September 1990 from Site 1 in the entrance channel, Sites 2 and 3 in Nornalup Inlet, and Site 4 in Walpole Inlet (Fig. 1). Sampling was carried out at night with two 0·5-mm-mesh conical nets, each 0·6 m in diameter and 2·0 m in length, attached to either side of a powerboat. The nets were towed just below the surface for 10 min, and the volume of water filtered by each net during each tow was determined by using digital flowmeters attached to the nets. After the completion of each tow, the nets were washed and the samples fixed in buffered 4% formaldehyde-seawater and later preserved in 70% ethanol. The above sampling procedure is the same as that used in comparable studies of larval fishes in the Swan Estuary and Wilson Inlet in south-western Australia (Neira and Potter 1992*b;* Neira *et al.* 1992). The surface temperature and salinity were recorded monthly at each site prior to sampling. The direction of the tidal movement was not taken into account because sampling was carried out at night, at which time either flood or ebb tides could have occurred.

Fish larvae were separated from samples under a stereomicroscope, identified to the lowest possible taxon and counted. The term larva incorporates the yolk-sac, preflexion, flexion and postflexion stages as described by Leis and Trnski (1989). Larvae were identified to family, genus and species by using the descriptions of related taxa given in Fahay (1983), Leis and Rennis (1983), Moser *et al.* (1984), Okiyama (1988) and Leis and Trnski (1989). The few larvae that could not be identified to any taxonomic level were placed in the 'unidentified' category.

Life-cycle Categories

Each species caught as larvae was assigned to one of the following four life-cycle 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 as either larvae, juveniles or adults; *(iii)* estuarine (E), i.e. spawns within estuaries and *(iv)* freshwater (F), i.e. spawns in the freshwater region of rivers (see Lenanton and Potter 1987). The allocation of each species to one of these categories follows the designations given in Potter *et al.* (1990), except in the cases of *Favonigobius lateralis* and *Leptatherina presbyteroides*, which have been shown to spawn within the nearby Wilson Inlet as well as in marine waters (Neira and Potter 1992*b*; Potter *et al.* 1993).

Analysis of Data

The total number of all fish larvae and the total number of larvae of each species caught in both nets at each site in each month were converted to a concentration, i.e. the number of larvae per 100 m^3. The

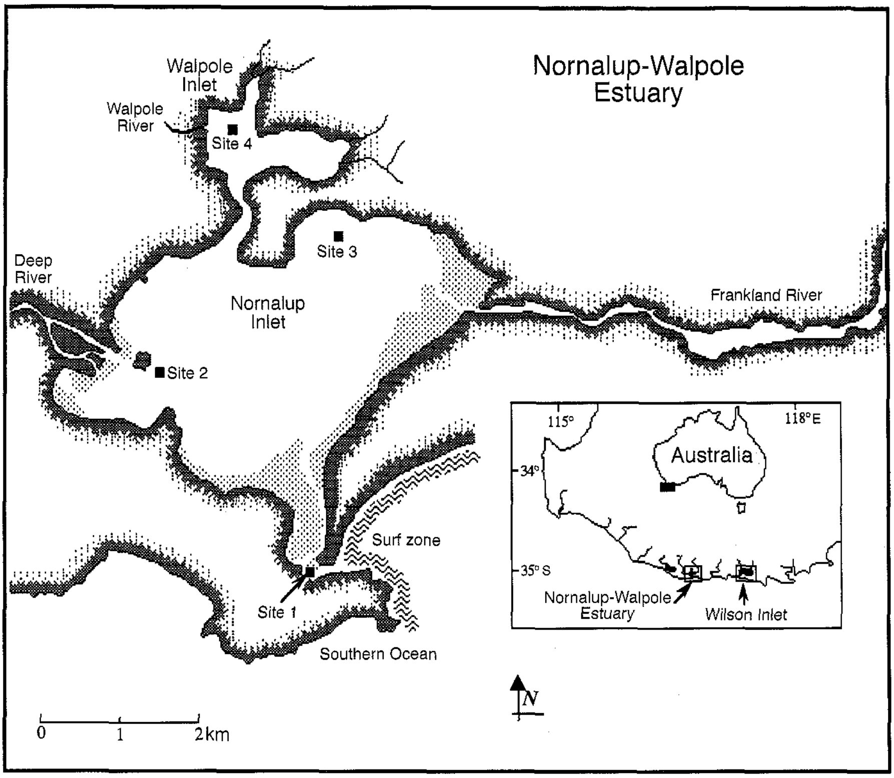

Fig. 1. Map of the Nornalup–Walpole Estuary on the southern coast of Western Australia, showing the location of the sampling sites in the entrance channel (Site 1), Nornalup Inlet (Sites 2 and 3) and Walpole Inlet (Site 4). The inset shows the location of Wilson Inlet relative to the Nornalup–Walpole Estuary.

concentrations in each sample of both the total number of larvae and the total number of each species at each site in each of the 12 months were then summed. These values were used to calculate the percentage contributions made by the larvae of each family and species in the whole system and by each species at each of the four sampling sites and the percentage contributions made by the numbers of larvae representing species in each life-cycle category in the whole system and at each site. The mean monthly values for the concentration of larvae and the number of species (Fig. 2) were calculated by using data obtained from all four sampling sites. The numbers of species in each month at each of the four sites (Fig. 3) represent the numbers recorded in the two nets on each sampling occasion. The total numbers of larvae of individual species in each month and at each site (Figs 4 and 5) represent the sum of their concentrations at all four sampling sites in each of the 12 months of sampling (Fig. 4) and in each of the 12 months at each site, respectively (Fig. 5).

Classification and ordination were undertaken to determine the degree of similarity of the larval fish assemblages at the four sampling sites between November 1989 and March 1990, i.e. during the time when most larvae were caught. The analyses were carried out with the pattern analysis package (PATN) of Belbin (1987) and used the mean concentrations of the larvae of those species that contributed ≥0·1% to the total number of larvae caught during the study (see Table 1). The matrix of species concentration × site was subjected to the range standardization option of PATN and then transformed into an association matrix using the Bray–Curtis measure of dissimilarity. The resultant data set was used for classification by employing Unweighted Flexible Pair-Group Arithmetic Averaging (UPGMA, ß=0) and for ordination using Semi-Strong Hybrid (SSH) multidimensional scaling. A Bray–Curtis percentage value of 100 means complete dissimilarity.

Table 1. Families and species of fish collected as larvae within the Nornalup–Walpole Estuary between October 1989 and September 1990, and their respective ranks according to their contributions to the total abundance

Values given for each family and species in the 'Total contribution' column correspond to the total sum of the numbers per 100 m^3 for all of the 12 months of sampling. The percentage contributions of each family and species for the whole system (in parentheses) were calculated from these above values and are given only when contributions are ≥0.1% (see Materials and Methods for further details). The totals in the penultimate column correspond to the non-adjusted, total numbers of larvae caught during the study. Life-cycle categories: E, estuarine; F, freshwater; O, marine estuarine-opportunist; S, marine straggler

Family rank	Family and species	(Species rank)	Total contribution Family (%)	Total contribution Species (%)	Contribution per site (%) 1	2	3	4	Total	Life-cycle category
1	Engraulididae		2765 (56·7)							
	Engraulis australis	(1)		2765 (56·7)	11·6	64·1	52·2	51·0	7030	E
2	Gobiidae		1930 (39·6)							
	Pseudogobius olorum	(2)		1188 (24·4)	13·2	23·4	17·7	35·4	2982	E
	Favonigobius lateralis	(3)		729 (15·0)	50·9	10·7	25·3	8·6	1922	E
	Favonigobius suppositus	(8)		9 (0·2)				0·9	37	E
	Gobiid	(12)		4 (0·1)	2·1				13	S
3	Syngnathidae		44 (0·9)							
	Urocampus carinirostris	(5)		43 (0·9)	0·7	0·4	0·5	2·6	101	E
	Syngnathid	(32)		1	0·2				1	S
4	Atherinidae		39 (0·8)							
	Atherinosoma elongata	(4)		36 (0·7)	1·3	0·2	2·3	0·3	106	E
	Leptatherina presbyteroides	(15)		2 (0·1)	0·5	<0·1			6	O
	Atherinomorus ogilbyi	(24)		1	0·3	<0·1			3	S
5	Blenniidae		26 (0·5)							
	Parablennius tasmanianus	(6)		26 (0·5)	2·2	0·4	0·5	0·6	36	E
6	Terapontidae		22 (0·5)							
	Pelates sexlineatus	(7)		22 (0·5)	0·5	0·5	0·7	<0·1	57	O
7	Clupeidae		10 (0·2)							
	Spratelloides robustus	(9)		7 (0·1)	4·7	<0·1			25	S
	Sardinella lemuru	(15)		2	1·1				6	S
	Hyperlophus vittatus	(21)		1	0·3			<0·1	4	O
8	Galaxiidae		7 (0·1)							
	Galaxias occidentalis	(9)		7 (0·1)		<0·1	0·2	0·3	25	F
8	Platycephalidae		7 (0·1)							
	Platycephalus speculator	(11)		7 (0·1)	0·2	0·1	0·2	0·2	20	E

10	Sillaginidae		4 (0·1)							
	Sillago spp·	(13)		4 (0·1)	1·6	<0·1	0·1		11	S
11	Gobiesocidae		3 (0·1)							
	Gobiesocid I	(18)		1	0·5		<0·1		5	S
	Gobiesocid III	(24)		1	0·5				3	S
	Gobiesocid II	(32)		0·5	0·2				1	S
	Gobiesocid IV	(32)		0·5	0·2				1	S
13	Labridae		2							
	Pseudolabrus spp·	(15)		2	0·8	<0·1	<0·1		6	S
	Labrid	(28)		0·5	0·4				2	S
13	Monacanthidae		2							
	Meushenia spp·	(21)		1	0·2	<0·1	<0·1		4	S
	Monacanthid	(32)		0·5	0·2				1	S
13	Pempherididae		2							
	Pempheris multiradiata	(18)		2	0·4		0·1		5	S
13	Clinidae		2							
	Cristiceps australis	(18)		2	1·0		<0·1		5	S
17	Scomberesocidae		1							
	Scomberomorus australasicus	(21)		1	0·8				4	S
17	Carangidae		1							
	Pseudocaranx dentex	(24)		1	0·2	<0·1			3	S
17	Callionymidae		1							
	Callionymus sp·	(24)		1	0·7				3	S
17	Triglidae		1							
	Triglid	(28)		1	0·3	<0·1			2	S
17	Sparidae		1							
	Acanthopagrus butcheri	(28)		1			<0·1	<0·1	2	E
17	Scorpaenidae		1							
	Scorpaenid	(28)		1	0·5				2	S
17	Hemiramphidae		1							
	Hyporhamphus melanochir	(32)		1		<0·1			1	E
24	Tetraodontidae		0·5							
	Tetraodontid	(32)		0·5	0·3				1	S
	Unidentified			3(0·1)	1·6		0·1		11	S
	Total (per 100 m^3)			4874	143	2473	1177	1081		
	(%)				(2·9)	(50·7)	(24·2)	(22·2)		
	Total (non-adjusted)								39 068	

Results

Environmental Variables

In each month, the surface salinities were usually highest at Site 1 in the entrance channel and lowest at Site 4 in Walpole Inlet (Fig. 2). The surface salinity at Site 1 increased from 28·7 to 35·7 between October 1989 and January 1990 and then declined to 2·0 in July before increasing to 23·1 in September 1990. The corresponding values for surface salinity at Site 4 followed similar trends but were considerably lower than those at Site 1 in both spring and middle to late autumn (Fig. 2).

The water temperatures at the four sites in any given month were similar. Mean water temperatures for the four sites increased from 17·8°C to a maximum of 24·1°C between November 1989 and March 1990 and declined to a minimum of 10·7°C in July 1990 (Fig. 2).

Composition of the Larval Assemblage

In all, 39 068 fish larvae, belonging to 36 species and representing 23 families, were caught at the four sites in the Nornalup–Walpole Estuary between October 1989 and September 1990 (Table 1). Fourteen of the species were caught only at Site 1 in the entrance channel, whereas all but four of the species caught in the basin sites (Sites 2, 3 and 4) were also found at this entrance channel site (Tables 1 and 2). The larvae collected in the entrance channel accounted for only 2·9% of the total number of larvae in the whole system. The larvae caught at Site 2 accounted for 50·7% of the total, i.e. more than twice the contributions made by larvae at Site 3 (24·2%) and Site 4 (22·2%) (Table 2).

The larvae of three species contributed more than 96% of all larvae caught during the study. The engraulidid *Engraulis australis* was the most abundant of these species, contributing 56·7% to the total number of larvae, followed by the gobies *Pseudogobius olorum* (24·4%) and *Favonigobius lateralis* (15·0%) (Table 1). The other species that contributed ≥0·5% were the syngnathid *Urocampus carinirostris*, the atherinid *Atherinosoma elongata*, the blenniid *Parablennius tasmanianus,* and the terapontid *Pelates sexlineatus* (Table 1).

Table 2. Numbers of species and numbers of larvae representing each of the four life-cycle categories, and the percentage contributions of those categories to the larval fish assemblage of the whole Nornalup–Walpole Estuary and at each of the four sampling sites between October 1989 and September 1990

Numbers of larvae in each category in the whole system and at each sampling site correspond to the total sum of the numbers per 100 m^3 for all of the 12 months of sampling

Life-cycle category	Whole system		Entrance Site 1		Nornalup Inlet Site 2		Nornalup Inlet Site 3		Walpole Inlet Site 4	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Species										
Straggler	22	61·1	22	68·7	7	38·8	6	37·5	0	0·0
Opportunist	3	8·3	3	9·4	2	11·1	1	6·2	2	16·7
Estuarine	10	27·8	7	21·9	8	44·4	8	50·0	9	75·0
Freshwater	1	2·8	0	0·0	1	5·6	1	6·2	1	8·3
Total	36		32	88·9	18	50·0	16	44·4	12	33·3
Larvae										
Straggler	36	0·7	27	18·6	4	0·2	5	0·4		<0·1
Opportunist	26	0·5	2	1·4	15	0·6	8	0·7	1	0·1
Estuarine	4805	98·6	114	80·0	2453	99·2	1162	98·7	1076	99·5
Freshwater	7	0·1	0	0·0	1	<0·1	2	0·2	4	0·3
Total	4874		143	2·9	2473	50·7	1177	24·2	1081	22·2

Several of the species recorded as larvae at Site 1 in the entrance channel were marine species belonging to families such as the Clupeidae, Sillaginidae, Gobiesocidae, Labridae and Monacanthidae (Table 1). The larvae of marine species belonging to the Scomberesocidae, Callionymidae, Scorpaenidae and Tetraodontidae were found exclusively at Site 1. Although the larvae of the remaining eight families recorded at Site 1 were also represented only by marine species, they occurred in at least one of the sites in the basins of the estuary (Table 1).

Seasonal and Spatial Changes in Larval Fish Concentrations

The mean concentration of all larvae within the Nornalup–Walpole Estuary increased from 4 to 314 larvae per 100 m^3 between October 1989 and January 1990, before declining to 204 larvae per 100 m^3 in February and then rising again to 319 larvae per 100 m^3 in March (Fig. 2). Concentrations subsequently declined to <34 larvae per 100 m^3 in April and May of 1990. Few larvae were caught in the winter months, i.e. June to August. The peaks in January and March of 1990 were largely due to the high concentrations of *E. australis* larvae (Fig.4).

The mean number of species recorded as larvae at the four sites in the estuary followed a trend similar to that exhibited by the larval concentrations, increasing from two to 13 between October 1989 and January 1990 and then declining to six to eight between February and April and to less than one in each of the three winter months (Fig. 2).

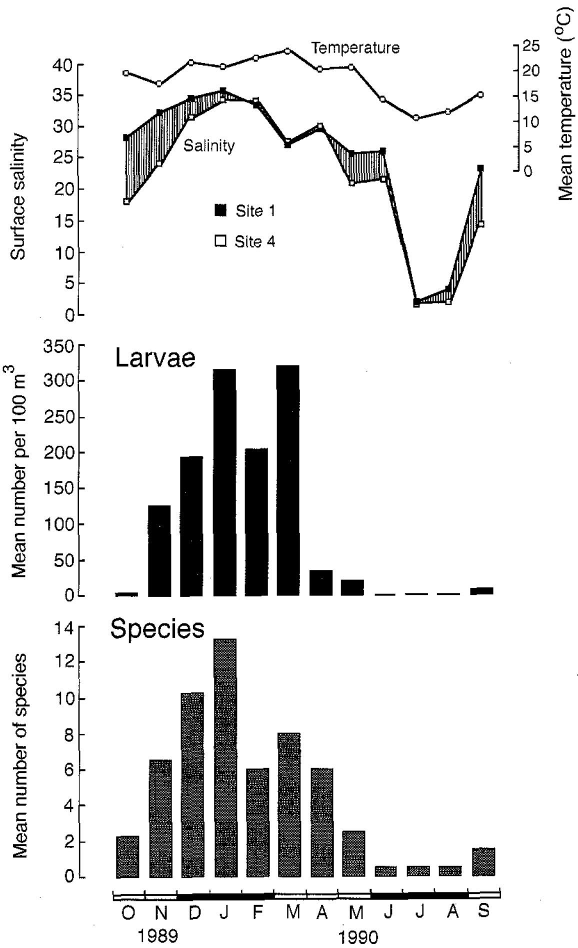

Fig. 2. Monthly salinities at Sites 1 and 4, mean monthly surface water temperatures, mean monthly concentrations of fish larvae (numbers per 100 m^3) and mean monthly numbers of species in the Nornalup–Walpole Estuary between October 1989 and September 1990. Shading in salinity curve indicates the difference between surface salinities at Site 1 (entrance channel) and those at Site 4 (Walpole Inlet). In this and Figs 3 and 4, the black bars on the horizontal axis denote summer and winter months and the open bars the spring and autumn months.

Although fish larvae were caught only between November and April at Site 1 in the entrance channel, they were collected in most months at Sites 2 and 3 in Nornalup Inlet and in each of the 12 months of the study at Site 4 in Walpole Inlet (Fig. 3). The number of marine species was greatest in December (10 species) and January (11 species) at Site 1 (Fig. 3), when salinities at that site had reached 35·7 (Fig. 2).

Most of the larvae of each of the three most abundant species (*E. australis, P. olorum* and *F. lateralis*) were caught between November 1989 and March 1990, with the concentrations reaching a maximum between January and March of 1990 (Fig. 4). The peaks in the concentrations of *E. australis* larvae in January and March (Fig. 4) were due to the large numbers of this engraulidid at Site 2 in those months (i.e. 590 and 380 larvae per 100 m^3, respectively) and occurred at water temperatures of 20·6°C and 24·5°C and salinities of 34·9 and 26·3, respectively. The peak in the concentration of *P. olorum* larvae in February was due to the large catch of this gobiid also at Site 2, at a temperature and salinity of 22·5°C and 33·1, respectively. Similar summer to early-autumn peaks in concentration were exhibited by the larvae of three other estuarine species (*P. tasmanianus, A. elongata* and *U. carinirostris*) and by the larvae of the only marine species (*P. sexlineatus*) that was even moderately abundant in the estuary (Fig. 4).

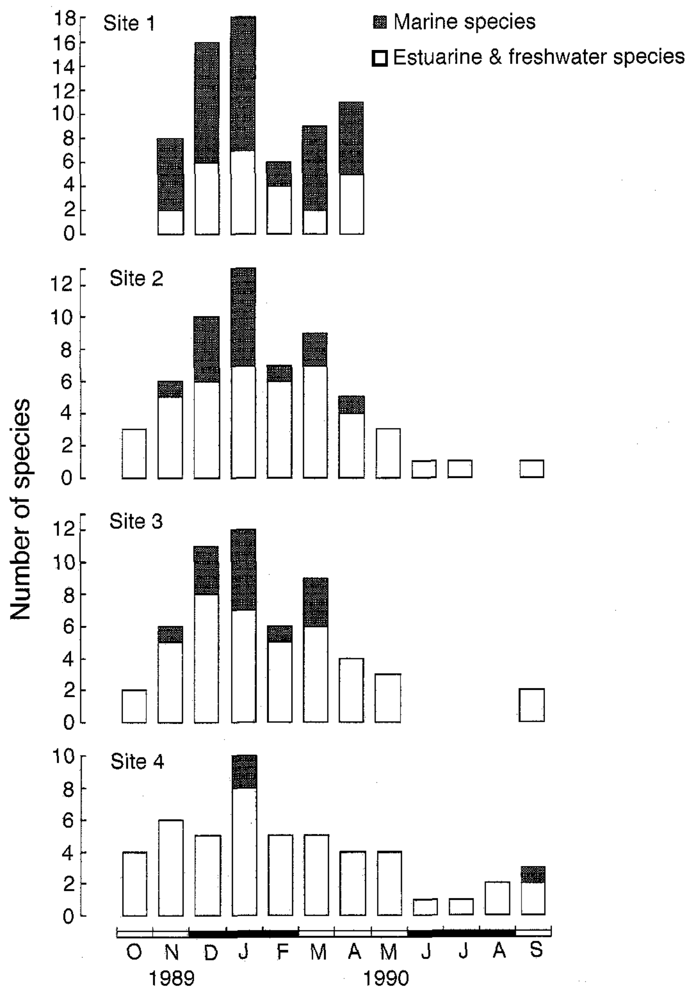

Fig. 3. Numbers of species recorded as larvae at each of the four sampling sites in the Nornalup–Walpole Estuary between October 1989 and September 1990. Stippled area in each bar indicates species spawned at sea, i.e. those assigned to the life-cycle categories of marine straggler and marine estuarine-opportunist.

Although the larvae of each of the seven most abundant species were recorded at all four sites, they were always least abundant at Site 1 and most numerous at Sites 2 or 3 except for *U. carinirostris,* which was most abundant at Site 4 in Walpole Inlet (Fig. 5).

Life-cycle Categories

The 36 species caught as larvae throughout the estuary comprised 22 species of marine straggler, three species of marine estuarine-opportunist, 10 estuarine species and one freshwater species (Tables 1 and 2). The number of species of marine straggler recorded at the four sites declined from 22 at Site 1 to seven and six at Sites 2 and 3, repectively, to none at Site 4. In contrast, the number of estuarine species increased from seven at Site 1 to eight at Sites 2 and 3 to nine at Site 4. The single freshwater species (*Galaxias occidentalis*) was recorded at all but Site 1 in the entrance channel (Table 1).

The larvae of marine stragglers, marine estuarine-opportunists and freshwater species contributed only 0·7%, 0·5% and 0·1%, respectively, to the total number of larvae in the whole system (Table 2). In contrast, the larvae of estuarine species contributed 98·6% to that total. The larvae of marine species (marine stragglers and marine estuarine-opportunists) accounted for 20·0% of the total at Site 1 in the entrance channel but only between <0·1 and 1·1% of the totals caught at any of the three basin sites (Table 2). Conversely, the contribution of estuarine-

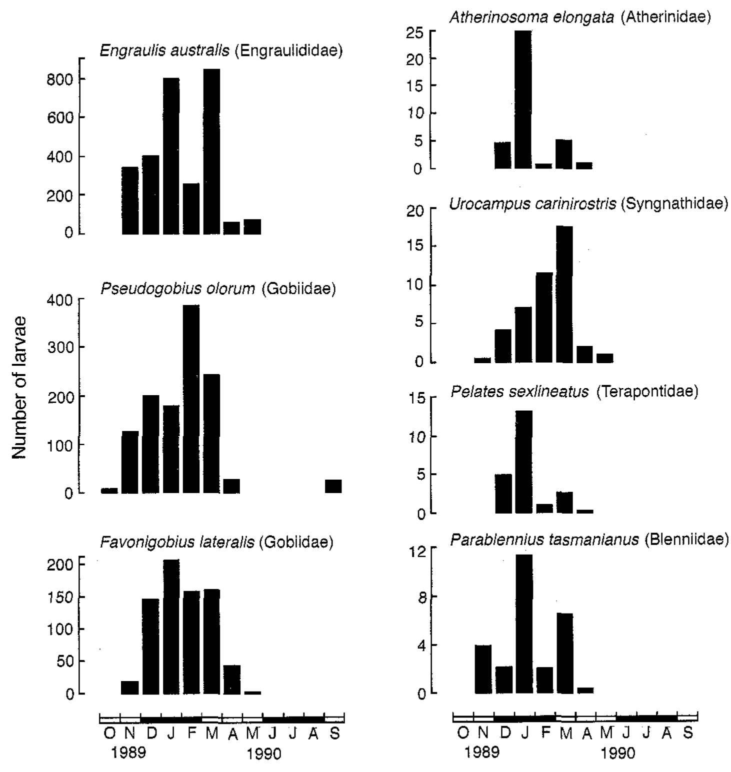

Fig. 4. Total numbers of larvae of the seven most abundant species in the Nornalup–Walpole Estuary in each month between October 1989 and September 1990. Each bar represents the sum of the numbers per 100 m^3 at the four sampling sites. In this and Fig·5, the species have been arranged in decreasing order of abundance and, except for *Pelates sexlineatus*, all belong to the estuarine life-cycle category.

spawned larvae to the total caught at each site was greater at Sites 2, 3 and 4 (98·7% to 99·5%) than at Site 1 in the entrance channel (80·%).

Classification and Ordination of Larval Fish Assemblage

Classification and ordination of the samples taken at the four sites in the Nornalup–Walpole Estuary between November 1989 and March 1990, i.e. the months when larvae were most abundant, separated the larval fish assemblage at Site 1 in the entrance channel from those of the three basin sites (Fig. 6). Classification separated the larval assemblage from Site 1 in December, January and February from those of the same site in November and March, in which months the samples were most dissimilar. The larval assemblages from basin Sites 2, 3 and 4 in all months except Site 4 in November and Site 2 in January tended to cluster together, with those in December, February and March at Site 4 forming a distinct group (Fig. 6).

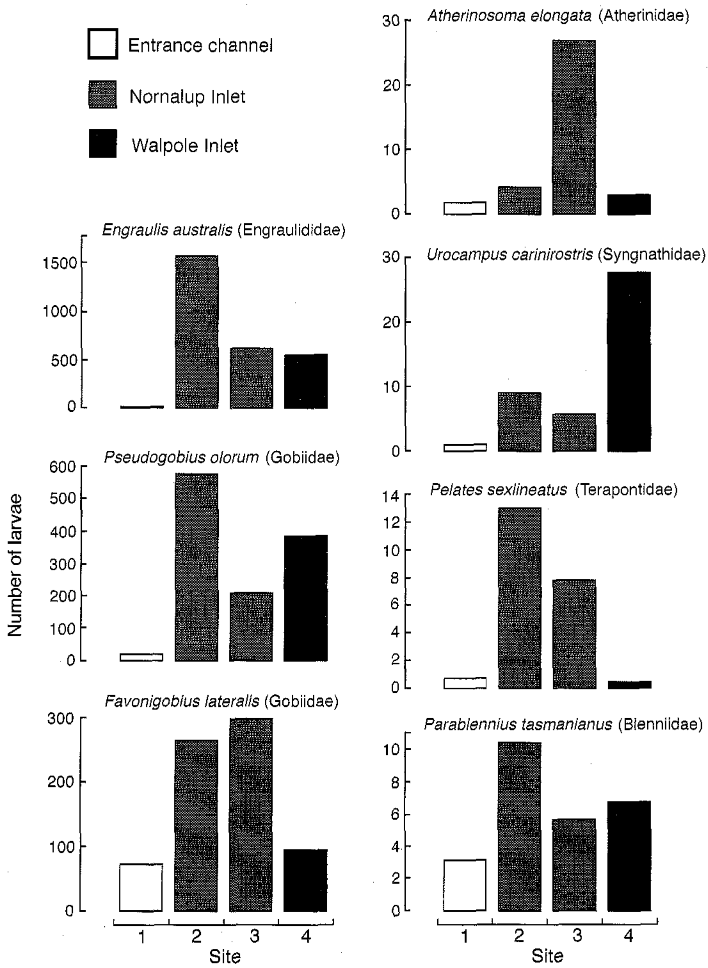

Fig. 5. Total numbers of larvae of the seven most abundant species in the Nornalup–Walpole Estuary at each sampling site. Each bar represents the sum of the numbers per 100 m^3 in the 12 months between October 1989 and September 1990.

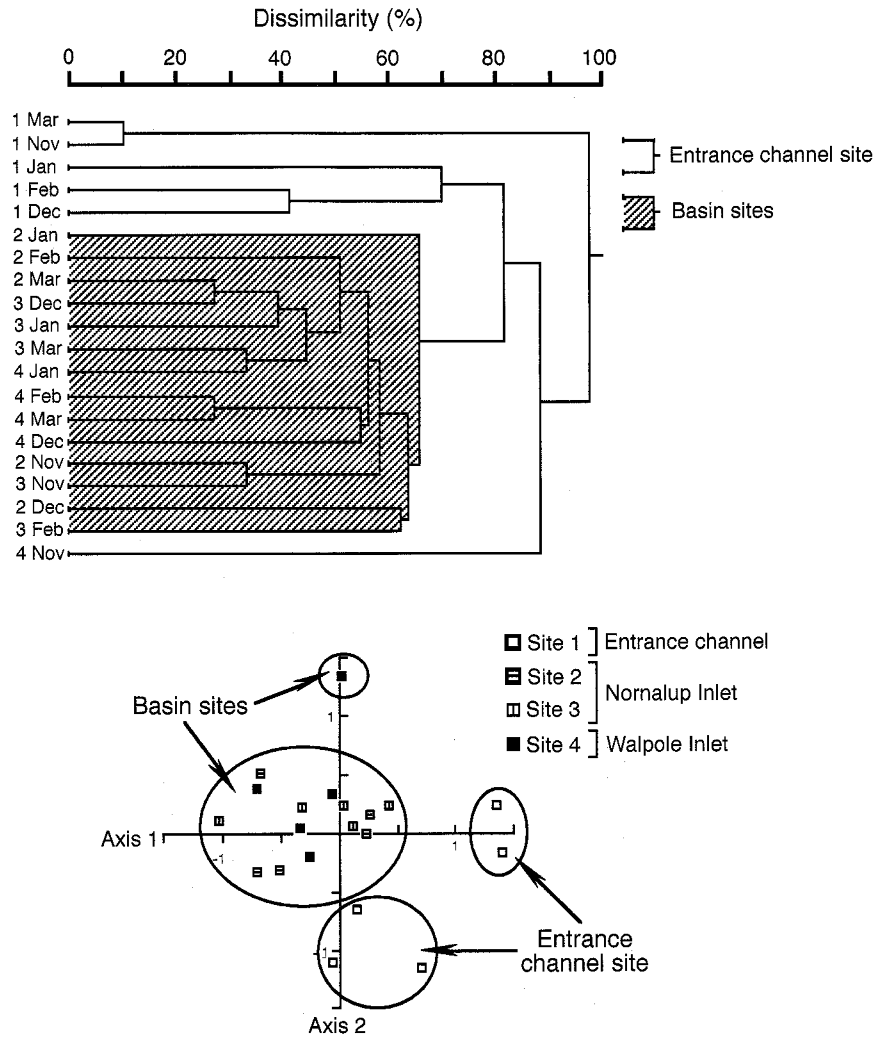

Fig. 6. Classification and ordination (Vector 1 *v.* Vector 2) of the samples collected at the four sampling sites in the Nornalup–Walpole Estuary in each month between November 1989 and March 1990. Numbers preceding the months in the dendrogram are site numbers.

Discussion

Species Composition

The present study showed that the total numbers of families and species found as larvae in the two basins of the Nornalup–Walpole Estuary (19 and 24, respectively) were virtually identical to those recorded by Neira and Potter (1992*b*) in the basin of the nearby and seasonally closed Wilson Inlet (17 and 25, respectively). However, the overall number of species recorded in the estuarine category was higher in Wilson Inlet (16 *v.* 10). Although the higher number of estuarine species in Wilson Inlet may in part reflect the longer sampling period (20 *v.* 12 months) and the larger area of this system (48 *v.* 13 km^2), it is also relevant that the extensive beds of the aquatic macrophyte *Ruppia megacarpa* in that system offer a greater diversity of fish habitats (Humphries *et al.* 1992; Humphries and Potter 1993).

The majority (25) of the total of 36 species found as larvae during the present study were marine species, of which 23 were never found as either juveniles or adults during a parallel study in the Nornalup–Walpole Estuary (Potter and Hyndes 1994). The species that dominated the larval assemblage in the two basins of the Nornalup–Walpole Estuary were also abundant in the basin of Wilson Inlet. Thus, the three most abundant species in the Nornalup–Walpole Estuary (*Engraulis australis, Pseudogobius olorum* and *Favonigobius lateralis*), which collectively contributed more than 95% to the total in the two basins, ranked second, first and sixth, respectively, in Wilson Inlet. In addition, larvae of the syngnathid *Urocampus carinirostris* ranked fifth in both systems and the blenniid *Parablennius tasmanianus*, which ranked sixth in the Nornalup–Walpole Estuary, was also one of the most abundant species in Wilson Inlet (Neira and Potter 1992*b*).

Seasonal Trends in Larval Concentrations

The peak in the overall concentration of fish larvae in the Nornalup–Walpole Estuary and Wilson Inlet (Neira and Potter, 1992*a*) occurred between January and March, which was later than in the more northern Swan Estuary, where the peak occurred between October and January (Neira *et al.* 1992). However, the peaks in the concentrations of fish larvae in all three systems occurred at water temperatures between 20°C and 24°C. The concentrations of fish larvae in the Nornalup–Walpole Estuary followed seasonal trends similar to those recorded in the Swan Estuary and Wilson Inlet (Neira and Potter 1992*b;* Neira *et al.* 1992), and in other estuaries and inshore marine embayments elsewhere in temperate Australia (e.g. Jenkins 1986; Steffe and Pease 1988) and southern Africa (e.g. Melville-Smith and Baird 1980; Beckley 1986; Whitfield 1989*b*).

The larval concentrations of the two most abundant species caught in the present study, *E. australis* and *P. olorum*, peaked in the same months in the nearby Wilson Inlet, i.e. between January and March (Neira and Potter 1992*b*), but occurred earlier in the Swan Estuary, i.e. in October and December, respectively (Neira *et al.* 1992).

Contributions of Estuarine and Marine-spawned Larvae

The larvae of estuarine species numerically dominated the larval fish assemblage of the Nornalup–Walpole Estuary, with representatives of this life-cycle category accounting for 98.6% of all larvae. This extreme dominance by estuarine-spawned larvae parallels the situation found in Wilson Inlet (Neira and Potter 1992*b*) and the Swan Estuary (Neira *et al.* 1992).

Although the larvae of 25 marine species were caught at the four sampling sites in the Nornalup–Walpole Estuary, they collectively contributed only 1·2% to the total in the whole system and were mainly restricted to the entrance channel site. These findings parallel those in Wilson Inlet, in which only seven of the 51 marine species caught in the entrance channel were found within the basin of that system and in which they accounted for less than 0·1% of the total number of larvae (cf. Neira and Potter 1992*a*, 1992*b*). The distinct larval assemblage in the entrance channel (Site 1) in December, January and February, which was reflected in the classification and ordination analyses, was due to the presence of many marine species at that site in those months.

The contrast between the presence of larvae of a large number of marine species in the entrance channels of both the Nornalup–Walpole Estuary and Wilson Inlet and, in most cases, the absence of juveniles and adults of these species within the basins of these systems, indicates that these larvae have been passively transported from outside these estuaries on flood tides. Moreover, the fact that the entrances of both estuaries are bounded by moderately strong surf zones and that most of the larvae of these typically inshore-marine species were caught at the preflexion stage, i.e. poorly developed (Neira and Potter 1992*a*; Neira, unpublished), suggests that these larvae were being transported into these systems from the surf zones. In this context, it is worth noting that several marine estuarine-opportunist species that use the Swartvlei Estuary (southern Africa) as a nursery area were also abundant as postlarvae in the surf zone outside that estuary (Whitfield 1989*a*, 1989*c*). In contrast to the situation in the Swartvlei Estuary, however, the larvae of only one species caught in the entrance channel of the Nornalup-Walpole Estuary belonged to species that are moderately abundant as juveniles within this system (Potter and Hyndes 1994).

The only marine estuarine-opportunist species that was found as larvae in the entrance channel and also at each of the three basin sites of the Nornalup–Walpole Estuary was the terapontid *Pelates sexlineatus*. The fact that the majority of these larvae were caught at Sites 2 and 3 in Nornalup Inlet indicates that, if these larvae were spawned outside, then the tidal flow into the estuary might be sufficiently strong to transport them passively into that part of the system. However, because the adults of this terapontid are moderately abundant in the estuary (Potter and Hyndes 1994), it is also possible that these larvae were spawned within this system.

Is There Recruitment of Marine Species as Larvae?

The present study showed that, apart from possibly *P. sexlineatus*, none of the other 13 teleost fish species regarded as marine estuarine-opportunists in the Nornalup–Walpole Estuary by Potter and Hyndes (1994) are recruited into this estuary as larvae, even though this system is permanently open to the sea by a short, moderately deep channel through which there is a constant tidal exchange throughout the year (Hodgkin and Clark 1988). Thus, marine species such as the arripid *Arripis georgianus*, the sillaginid *Sillaginodes punctata* and the sparid *Pagrus auratus*, which are abundant in this system (Potter and Hyndes 1994), are recruited at the juvenile and/or adult stages. Except for the few postflexion larvae of sparids and clupeids caught entering the nearby Wilson Inlet on flood tides (Neira and Potter 1992*a*), the number of larvae of other marine estuarine-opportunists in that system was very low, even when in the second year of the study the mouth and the 1-km-long entrance channel of Wilson Inlet remained open throughout the whole summer (Neira and Potter 1992*a*, 1992*b*).

The conclusion that marine estuarine-opportunist species are typically recruited into the Nornalup–Walpole Estuary and Wilson Inlet as juveniles or adults, rather than as larvae, parallels the situation recorded by Lenanton (1977) in the Blackwood River Estuary, approximately 150 km west of Nornalup on the southern coast of Western Australia. Although these results indicate that the marine species that are abundant in these estuaries complete their larval life at sea before entering these systems, there are at present no data on the location and type of marine habitat occupied by these larvae.

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