Estuarine, Coastal and Shelf Science (1992) **35**, 213–224

Notes and Discussion

Movement of Larval Fishes Through the Entrance Channel of a Seasonally Open Estuary in Western Australia

Francisco J. Neira[a] and Ian C. Potter

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

Received 22 August 1991 and in revised form 20 December 1991

Keywords: estuaries; fish larvae; transport; Western Australian coast

Approximately 5300 fish larvae, representing 59 species and 39 families, were collected in flood and ebb tide samples taken by plankton and beach seine nets in the narrow entrance channel of a seasonally open estuary (Wilson Inlet), in the two to three months before the mouth became closed by a sand bar. All of the species were recorded on flood tides and eight of the nine that were also found in ebb tides were spawned within the estuary. The other 51 species belonged to teleosts which typically breed at sea. The most abundant species caught during this study (*Favonigobius lateralis*) was flushed out of the estuary as preflexion larvae on ebb tides and then re-recruited as postflexion larvae on flood tides. While other species which spawn within the estuary (e.g. *Pseudogobius olorum*, *Engraulis australis* and *Urocampus carinirostris*) were also flushed out on ebb tides, they rarely returned on flood tides as postflexion larvae. Of the 51 marine species, 35 were not collected as either juveniles or adults within the estuary. These species were caught only on flood tides and mainly as preflexion larvae. In contrast, the sparids *Pagrus auratus* and *Rhabdosargus sarba*, which occur as juveniles in the estuary, were found entering the entrance channel on flood tides as postflexion larvae. The fact that the last two species are amongst the few teleosts that might be recruited as larvae into the main body of the estuary, reflects the very small tidal movement in that part of the system.

Introduction

The majority of fish species found in temperate estuaries breed at sea and typically enter these systems as either late larvae or juveniles (Cronin & Mansueti, 1971; Haedrich, 1983; Dando, 1984; Boehlert & Mundy, 1988). Those marine species which enter estuaries as larvae are generally transported into and through estuaries by passive and/or active tidal transport (Weinstein *et al.*, 1980; Fortier & Leggett, 1982; Norcross & Shaw, 1984; Boehlert & Mundy, 1988; Drake & Arias, 1991). Although only relatively few teleosts complete their life cycles within estuaries, these sometimes attain very large numbers in

[a]Author to whom correspondence should be sent.

0272–7714/92/080213 + 12 $03.00/0

these systems (e.g. Claridge *et al.*, 1986; Loneragan & Potter, 1990; Potter *et al.*, 1990; Whitfield, 1990).

Several of the estuaries on the southern coast of Western Australia, such as Wilson Inlet, are bounded by surf zones and become seasonally closed off from the sea through the formation of sand bars at their mouths (Lenanton & Hodgkin, 1985; Hodgkin & Clark, 1988). Since the entrance channels of these estuaries are narrow and shallow and the range in tidal height in south-western Australia is only about 1 m (Hodgkin & Di Lollo, 1958), only a small amount of marine water moves through these channels into the shallow basins of the estuary during the period when the estuary is open to the sea. This suggests that, in comparison with typical northern hemisphere estuaries, the opportunities for larval fishes to be transported into and through these estuaries by tidal action are more limited. On the other hand, the relatively small tidal influence within the basins of these estuaries suggests that the larvae produced by estuarine species are less likely to be swept out to sea.

The present study on fish larvae within the short entrance channel of Wilson Inlet was undertaken to elucidate the extent to which species are being transported within this channel on the flood and ebb tides, respectively, and at what developmental stages, i.e. as preflexion or postflexion larvae. The data obtained are then considered in the context of the results of extensive beach seine, gill net and otter trawl sampling in Wilson Inlet (Potter *et al.*, in prep.), to determine which of the marine species subsequently remain within this system and transform into juveniles. Emphasis has also been placed on examining the hypothesis that, because of the greater number of species that spawn at sea rather than in estuaries, the number of species caught as larvae should be greater on flood than ebb tides. This hypothesis is particularly relevant as the surf zone immediately outside Wilson Inlet represents the type of environment often utilized by the early development stages of certain marine teleost species (e.g. Ruple, 1984; Kinoshita, 1986; Whitfield, 1989*a*).

Materials and methods

Study area and sampling regime

Wilson Inlet is a shallow estuary (generally <2 m deep), which occupies an area of 48 km^2 on the southern coast of Western Australia (Hodgkin & Clark, 1988). The narrow mouth of this estuary becomes closed during the summer or autumn by a sand bar. This prevents the exchange of water between the entrance channel and the Southern Ocean, until the bar is artificially breached in the following August or September, when the water level within the system reaches a specified level. The short (c. 1 km) entrance channel becomes tidal approximately 2–4 weeks after the sand bar has been breached. During the present study, the width and depth of this channel ranged from approximately 15 to 25 m and from 1·0 to 2·5 m, respectively. Since the abundance of fish eggs and larvae in Wilson Inlet is greatest between the late spring and end of summer (Neira & Potter, 1992), the present study of the movement of larvae into and out of the entrance channel of Wilson Inlet was undertaken during this period. Samples were obtained at the maximal water height of 15 flood and 5 ebb tides, from a point about 15 m upstream from the estuary mouth. Water current speed was measured using a General Oceanics electronic flowmeter and salinity and temperature with a YEO-KAL salinity-temperature bridge. The small number of samples taken on ebb tides was because on most occasions the channel water was too shallow to sample.

Plankton samples were obtained by towing against the current a 2·0 m long and 0·6 m diameter, 0·5 mm mesh conical net, that was attached from beneath the bow of a small power boat. Three or four tows of 5 min. duration were carried out on each of the flood and ebb tides sampled over a distance of about 150 m within the channel. The net was washed after each tow and the samples fixed in 5% formalin-sea water and later preserved in 70% alcohol. The volume of water passing through the net during each tow was calculated from data recorded by a digital General Oceanics flowmeter in the mouth of the net.

The total number of larvae in each replicate sample was counted and converted to a concentration, i.e. numbers per 100 m^3. The means for the concentration of larvae and the number of taxa in all of the replicate samples collected on each flood and ebb tide were then calculated.

A 4 m long and 1·5 m deep, 1·0 mm mesh seine net, with a centrally located 0·5 mm conical net, was also used to catch fish larvae on six flood tides. Sampling on each of these flood tides involved holding the net against the current for 10 min. in water about 1·6 m deep and repeating this procedure three to five times. Sampling on ebb tides could not be undertaken using this method because of the large amounts of algae and other material that were constantly being swept out through the entrance channel at these times.

Identification and measurements of larvae

Fish larvae were removed from plankton tow and beach seine samples using a dissecting microscope, identified to the lowest possible taxon and counted. The term larva comprises the yolk sac, preflexion, flexion and postflexion stages as described by Leis & Trnski (1989). Larvae were identified using the descriptions of larvae given by Uchida *et al.* (1958), Russell (1976), Miller *et al.* (1979), Leis & Rennis (1983), Fahay (1983), Moser *et al.* (1984), Ozawa (1986), Okiyama (1988) and Leis & Trnski (1989). Body lengths (BL) of all larvae, i.e. the notochord length in yolk sac, preflexion and flexion larvae, and the standard length in postflexion larvae, were measured to the nearest 0·1 mm using an eyepiece micrometer in the dissecting microscope. For convenience, larvae were separated into preflexion (including yolk sac and flexion larvae) and postflexion stages in order to be able to compare the development stages caught on flood and ebb tides.

Results

Environmental variables

Current speeds in the mouth of the entrance channel ranged from 0·08 to 0·9 m s^{-1} on flood tides and from 0·5 to 0·8 m s^{-1} on ebb tides. Salinities and temperatures on flood tides ranged from 33·0–35·5‰ and 16·9–20·5 °C, respectively. The corresponding values for ebb tides ranged from 21·6–24·9‰ and 19·5–21·5 °C, respectively.

Species composition

A total of 4392 fish larvae, representing 54 species and 38 families, was collected in plankton tows on flood and ebb tides (Table 1). *Favonigobius lateralis* was by far the most abundant species, comprising 76·3% of the total number of larvae. *Pseudogobius olorum, Engraulis australis, Haletta semifasciata, Urocampus carinirostris, Leptatherina presbyteroides* and *Meushenia hippocrepis* were the next most abundant species, each contributing between 1·5 and 3·0% to the total catch. Approximately 80% of the larvae belonged to the Gobiidae, whereas none of the next five most abundant families (Odacidae, Engraulididae, Atherinidae, Syngnathidae and Monacanthidae) contributed more than 3·0%.

TABLE 1. Numbers and body lengths of fish larvae of the various species caught with the plankton net and beach seine net in the entrance channel of Wilson Inlet. The percentage occurrence of the different species taken by the plankton net in the 29 flood tide samples and 15 ebb tide samples is also given

Family and species	Plankton net				Beach seine	
	Flood (%)	Ebb (%)	Total caught	Size range (mm)	Total caught	Size range (mm)
1 Gobiidae						
Favonigobius lateralis[a]	96·6	73·3	3352	1·8–7·1	777	5·0–7·9
Pseudogobius olorum[a]	41·4	53·5	133	1·9–6·7	2	4·3–5·8
Favonigobius suppositus[a]	24·1	26·7	21	3·4–4·6	1	5·8
Unidentified gobiid					1	6·5
2 Odacidae						
Haletta semifasciata	20·7		89	1·4–4·2		
Odax acroptilus	10·3		32	2·6–4·9		
Neoodax balteatus	10·3		6	8·5–10·1	2	8·2–9·3
3 Engraulididae						
Engraulis australis[a]	24·1	73·3	109	1·8–12·7	1	14·0
4 Atherinidae						
Leptatherina presbyteroides[a]	41·4	26·7	68	4·6–7·9	5	7·5–26·0
Atherinosoma elongata[a]	37·9	53·3	28	5·1–7·3	8	5·0–6·8
Atherinomorus ogilbyi	10·3		3	6·7–11·6		
5 Syngnathidae						
Urocampus carinirostris[a]	48·3	73·3	86		4	
Lissocampus runa	6·9		2	12·1–13·0		
Syngnathus phillipi	3·4		1			
6 Monacanthidae						
Meushenia hippocrepis	41·4		63	2·1–14·8	1	5·8
Unidentified monacanthid	24·1		19	1·8–3·5		
Acanthaluteres vittager	10·3		3	3·4–13·6	1	5·6
Brachaluteres jacksonianus					1	4·0
7 Clupeidae						
Unidentified clupeid	27·6		55	2·6–4·2	10	2·7–3·7
Spratielloides robustus	13·8	6·7	5	15·4–16·0	42	14·0–19·0
Etrumeus teres	6·9		2	6·7–8·4	3	4·9–5·8
8 Scombridae						
Scomber australasicus	17·2		47	1·5–3·2	2	3·0–3·1
9 Sparidae						
Pagrus auratus	41·4		33	8·0–11·1	7	7·2–9·8
Rhabdosargus sarba	17·2		7	8·9–9·5	3	8·7–9·0
10 Pempherididae						
Pempheris multiradiata	27·6		35	2·0–3·5		
11 Serranidae						
Unidentified serranid	10·3		29	2·5–4·1		
Anthiine serranid					1	2·4
12 Mullidae						
Unidentified mullid	10·3		21	2·6–3·4		
Upeneichthys vlaminghi					1	22·0
13 Labridae						
Unidentified labrid	27·6		14	1·8–3·7		
Pseudolabrus sp.	10·3		4	7·5–9·0	9	8·7–9·5
14 Callionymidae						
Callionymus sp.	20·7		17	1·8–2·9		
15 Blenniidae						
Parablennius tasmanianus[a]	6·9	33·3	14	2·3–2·9		
16 Schindleriidae						
Unidentified schindleriid	10·3		14	1·9–3·2		
17 Gobiesocidae						
Unidentified pigmented type	6·9		9	2·5–3·2		
Unidentified unpigmented type	10·3		1	3·6–6·1	1	5·4

TABLE 1. *Continued.*

Family and species	Plankton net				Beach seine	
	Flood (%)	Ebb (%)	Total caught	Size range (mm)	Total caught	Size range (mm)
18 Sillaginidae						
Sillago sp.	10·3		9	3·1–4·9	1	9·5
19 Clinidae						
Cristiceps australis[a]	17·2		5	4·2–13·2	7	11·3–13·7
Ophiclinus gracilis	10·3		3	8·3–8·6		
20 Leptoscopidae						
Lesueurina sp.	17·2		8	1·8–8·0		
21 Triglidae						
Chelidonichthys kumu	17·2		7	2·5–4·1		
22 Exocoetidae						
Cheilopogon furcatus	6·9		5	5·9–6·8		
23 Creediidae						
?Unidentified creediid	10·3		4	2·3–3·6		
24 Scorpaenidae						
Unidentified scorpaenid	10·3		4	1·9–4·9		
25 Enoplosidae						
Enoplosus armatus	10·3		3	8·0–9·2	1	7·5
26 Paralichthyidae						
Psudorhombus jenynsii	6·9		2	7·4–7·5	4	7·3–9·0
27 Pleuronectidae						
Ammotretis sp.	3·4		2	2·0–3·0		
28 Tripterygiidae						
Lepidoblennius marmoratus	6·9		2	10·3–15·2	1	9·7
29 Kyphosidae						
Kyphosus cornellii	3·4		2	2·5–3·0		
30 Tetraodontidae						
Unidentified tetraodontid	6·9		2	1·7–2·3		
31 Sciaenidae						
Unidentified sciaenid	6·9		2	3·0–3·1		
32 Carangidae						
Unidentified carangid	3·4		1	6·1		
33 Mugildae						
Aldrichetta forsteri	3·4		1	3·5		
34 Myctophidae						
Unidentified myctophid	3·4		1	6·0		
35 Pinguipedidae						
Parapercis haackei	3·4		1	3·3		
36 Platycephalidae						
Platycephalus sp.	3·4		1	1·8		
37 Scomberesocidae						
Scomberesox saurus	3·4		1	13·2		
38 Terapontidae						
Pelates sexlineatus	3·4		1	8·0		
39 Anotopteridae						
Anotopterus pharao					1	3·8

[a]Denotes species which spawn within Wilson Inlet.

Some species were well represented in samples taken in plankton tows on both flood and ebb tides (Table 1). For example, *F. lateralis* was present in 96·6 and 73·3% of the 29 flood and 15 ebb tide samples, respectively. Although the larvae of *P. olorum, L. presbyteroides, U. carinirostris* and *Atherinosoma elongata* were less numerous, they each occurred in at least 26% of the samples taken on both flood and ebb tides. In contrast, moderately abundant species such as *H. semifasciata*, *M. hippocrepis*, *Scomber australasicus* and *Pagrus auratus*, were caught only on flood tides. Indeed, of the 54 species recorded in the plankton tows, over 83% were not found in any of the ebb tide samples. While all of the species recorded in plankton tows on ebb tides were also collected at some time on flood tides, the frequency of occurrence of some species (*P. olorum*, *E. australis*, *U. carinirostris*, *A. elongata* and *Parablennius tasmanianus*) was greater in ebb tide than flood tide samples (Table 1).

A total of 901 larvae, representing 28 species and 19 families, was caught in the 18 samples collected using the small beach seine on six flood tides (Table 1). The only family recorded in the seine net that was not present in plankton tows was the Anotopteridae. All of the species caught in the seine net were recorded in plankton tows, except for *Brachaluteres jacksonianus*, *Upeneichthys vlaminghi*, *Anotopterus pharao*, an unidentified gobiid and an anthiine serranid, each of which was represented by only one larva. The relatively high contribution made by preflexion *F. lateralis* to the beach seine catches (86·2%) paralleled the situation found with the samples taken by the plankton net on ebb tides. The only other relatively abundant species in seine net samples was *Spratelloides robustus* (Table 1).

Concentrations of larvae and number of species

The mean concentrations of fish larvae on both flood and ebb tides varied greatly (Figure 1). Thus, the maximum mean concentrations on flood tides ranged from 9·3 larvae per 100 m^3 on 17 January 1990 to 172·8 larvae per 100 m^3 on 21 November 1989. The corresponding values for the ebb tide ranged from 5·2 larvae per 100 m^3 on 13 December 1989 to 121·2 larvae per 100 m^3 on 18 January 1989. Similarly, the number of species varied far more markedly on flood than ebb tides. Thus, the maximum mean numbers of species on flood tides ranged from 3·3 on 12 December 1989 to 22·7 on 21 November 1989, but only from 2·7 on 13 December 1989 to 7·3 on 19 January 1989 on ebb tides (Figure 1).

The dominance of *F. lateralis* in most samples accounts for the similarity between the mean concentrations of this species and those of the total larval fish assemblage on most flood and ebb tides. However, during the flood tide on 21 November 1989, the mean concentration of *F. lateralis* was very low, whereas that of the total assemblage was very high. The high concentration of fish larvae on 21 November 1989 reflects the influx of a variety of marine species (26 out of 31), and in particular those of *H. semifasciata* and *M. hippocrepis*.

Size and stage of development of selected species

The modal length class of larval *E. australis* caught on flood tides (2–2·9 mm) was the same as on ebb tides (Figure 2). A few postflexion larvae of this species, ranging from 10 to 15 mm, were taken on both ebb and flood tides. The modal length class of *P. olorum* was also 2–2·9 mm on both flood and ebb tides. However, while the larvae of this species on the ebb tide were preflexion larvae and never exceeded 3 mm, those on the flood tide included a few postflexion larvae ranging up to 6·7 mm. The size distribution of the 493 *F. lateralis* larvae caught on ebb tides was very similar to that of *P. olorum* taken on ebb tides, and produced the same modal length class of 2–2·9 mm. In contrast, all but four of the 3616 *F. lateralis* obtained on flood tides were postflexion larvae, ranging from 5·1 to 7·1 mm in length, and exhibiting a very well defined modal length class at 6–6·9 mm. The majority of

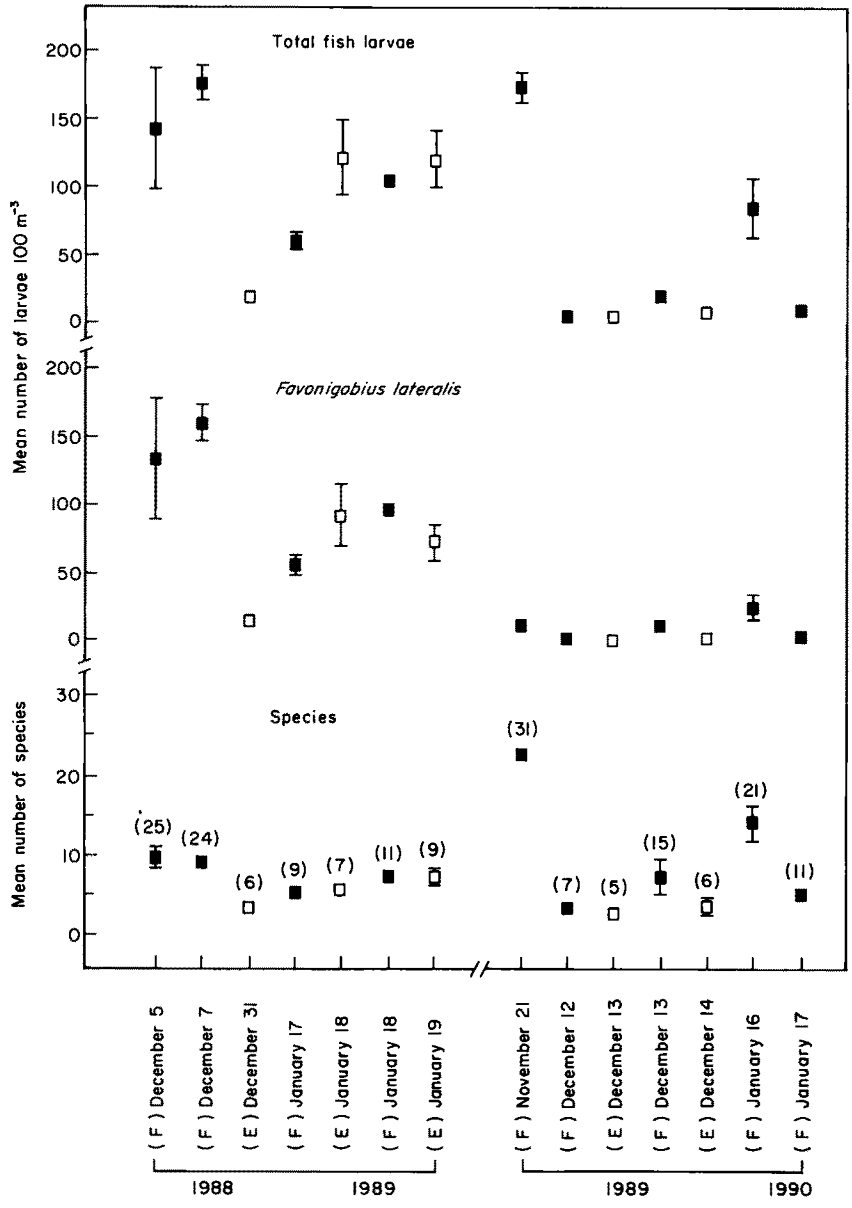

Figure 1. Mean (± 1 SE) for the concentration of fish larvae and number of species caught with the plankton net on flood and ebb tides in the entrance channel of Wilson Inlet during the 1988–89 and 1989–90 spawning seasons. Numbers in parentheses are the total numbers of species identified in all samples collected on each flood and ebb tide. The mean concentration (± 1 SE) of the most abundant species caught as larvae (*Favonigobius lateralis*) is also given. ■, Flood tide (F); □, ebb tide (E).

the *L. presbyteroides* were collected on flood tides and were largely represented by preflexion larvae with a modal length class of 5–5·9 mm (Figure 2).

All larvae of *S. australasicus*, *H. semifasciata* and *M. hippocrepis* were caught at the preflexion stage, except for a few postflexion representatives of the last species (Figure 2).

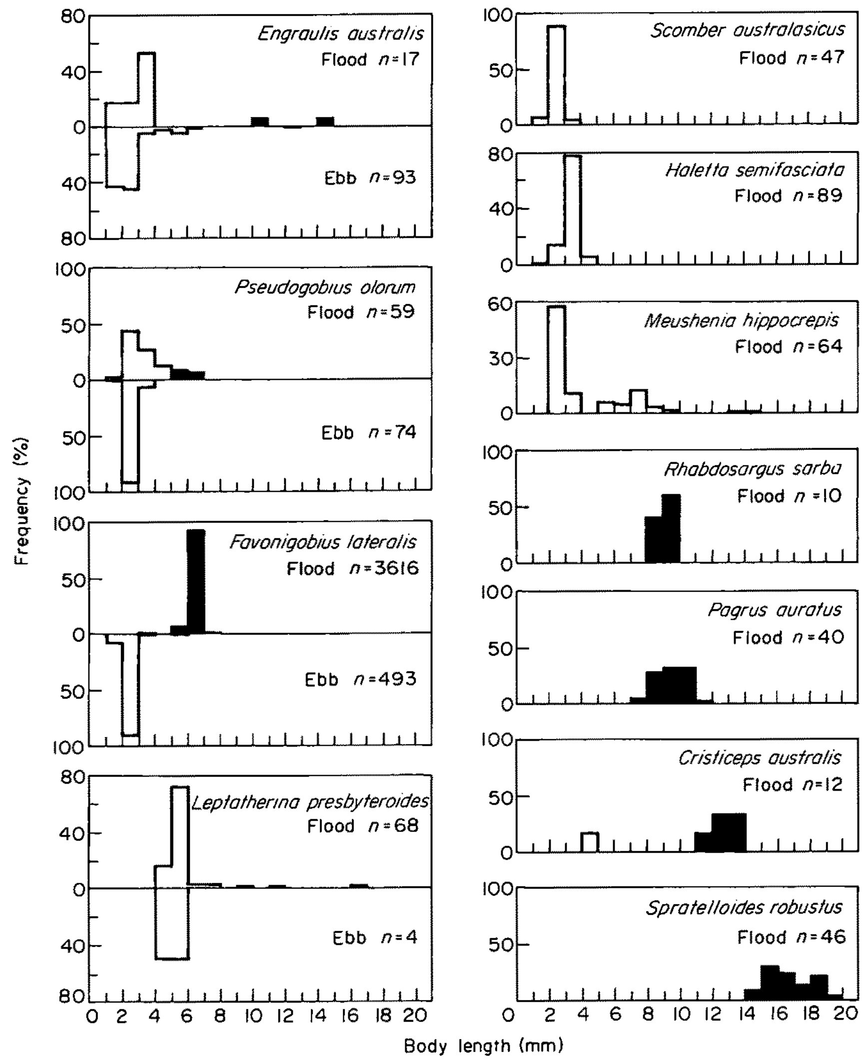

Figure 2. Length-frequency histograms for the larvae of selected species caught with the plankton net and beach seine net on flood and ebb tides in the entrance channel of Wilson Inlet. □, Preflexion larvae; ■, postflexion larvae.

The modal length class of each of these three species was well defined, lying between 2 and 4 mm. By contrast, larvae of *Rhabdosargus sarba, P. auratus* and *S. robustus* were collected exclusively at the postflexion stage (Figure 2).

Discussion

The number of species recorded on ebb tides (9) in Wilson Inlet was far lower than on flood tides (59). The adults of eight of the nine species recorded as larvae in ebb tides are known to breed within this and other estuaries in Southwestern Australia (Table 1; Potter *et al.*, 1983; Loneragan *et al.*, 1989; Loneragan & Potter, 1990; Neira *et al.*, 1992; Neira & Potter, 1992). Since there is little tidal movement of water within the basin of Wilson

Inlet (Hodgkin & Clark, 1988), the presence of larvae of these eight species in ebb tides in the entrance channel implies that they must have been produced by fish spawning near the lower end of the system. The ninth species caught as larvae on ebb tides, *Spratelloides robustus*, breeds at sea.

Although large numbers of larval *Favonigobius lateralis* were caught on both ebb and flood tides, those taken on outgoing tides were at the preflexion stage, whereas those caught on incoming tides were almost exclusively at the postflexion stage. This finding is consistent with the view that *F. lateralis* spawns within Wilson Inlet and indicates that appreciable numbers of this species are flushed out of the system as preflexion larvae and then return as postflexion larvae on the flood tides. This type of re-recruitment of *F. lateralis* into Wilson Inlet parallels that exhibited by the postflexion larvae of the gobiids *Psammogobius knysnaensis* and *Caffrogobius* spp. in the Swartvlei Estuary in southern Africa (Whitfield, 1989*b*), and of an unidentified gobiid species in Whangateau Harbour in New Zealand (Roper, 1986).

The observation that larvae of *P. olorum, E. australis* and *U. carinirostris* occurred more frequently on ebb than flood tides indicate that these species spawn predominantly within Wilson Inlet. All three species also breed within the large Swan Estuary (Neira *et al.*, 1992) and the second is also known to spawn within estuaries in Eastern Australia (Blackburn, 1950; Arnott & McKinnon, 1985).

During the present study, 49 of the 59 species were recorded only during flood tides and all of these belonged to marine teleosts, i.e. species which spawn at sea (Potter *et al.*, 1990). The most numerous of these larvae belonged to species such as the odacids *H. semifasciata* and *Odax acroptilus*, the monacanthid *M. hippocrepis*, the scombrid *S. australasicus*, the pempheridid *P. multiradiata*, and the sparid *P. auratus*. All of these species are abundant in the coastal waters of Southwestern Australia (Hutchins & Swainston, 1986).

Thirty five of the above 49 marine species caught in floodtide samples were never found as larvae, juveniles or adults during extensive sampling carried out at sites throughout Wilson Inlet using plankton tows, beach seines, gill nets and otter trawls over 20 consecutive months between 1987 and 1990 (Neira & Potter, 1992; Potter *et al.*, in prep.). Moreover, these 35 species are absent or at best rare in other estuaries of Southwestern Australia (Lenanton, 1977; Potter *et al.*, 1983; Loneragan *et al.*, 1989). Preflexion larvae of four of these species (*H. semifasciata, S. australasicus, P. multiradiata* and *M. hippocrepis*) were collected in numbers on flood tides. Since these species were caught neither as larvae on ebb tides nor as juveniles or adults within Wilson Inlet, the larvae of these species presumably do not survive after they have entered the estuary. It is therefore concluded that, while these locally abundant marine species typically settle in nearshore marine areas after completing their larval development, they can occasionally be passively transported into the estuary as preflexion larvae, probably from the surf zone immediately outside the estuary mouth.

In contrast to the situation with the larvae of the above four marine species, those of the sparids *P. auratus* and *R. sarba* were collected only as postflexion larvae and only in flood tides. Since both of these species occur as juveniles within Wilson Inlet and were never caught as larvae on ebb tides, some of the juveniles of both species found in the basin of Wilson Inlet may have been recruited as larvae. Moreover, the fact that the larvae of sparids, including those of *R. sarba*, are known to occupy surf zones in various parts of the world (Kinoshita, 1986; Whitfield, 1989*a*), suggest that, after completing their early development within the surf zone outside the mouth of Wilson Inlet, some of the larvae of the above two species are recruited into the estuary. This would parallel the recruitment pattern of *Rhabdosargus holubi* in southern African estuaries (Beckley, 1985; Whitfield, 1989*b*) and of *Acanthopagrus australis* in Australian estuaries (Pollock *et al.*, 1983; Miskiewicz, 1986).

Comparisons between the composition of the larval fish assemblage in the entrance channel with that of the larvae, juveniles and adults of teleost fishes within Wilson Inlet, emphasize that none of the more abundant teleosts found within the large basin of this system have been recruited into the system as larvae. This contrasts with the situation in many northern hemisphere estuaries where larvae enter and move through these systems by passive and/or active tidal transport (Weinstein *et al.*, 1980; Fortier & Leggett, 1982; Norcross & Shaw, 1984; Boehlert & Mundy, 1988; Drake & Arias, 1991). It is thus relevant that, in contrast to most of those estuaries, the tidal height outside Wilson Inlet is small and the entrance channel of this system is shallow and narrow (Hodgkin & Clark, 1988). Thus, while tidal water movement can transport larvae into the entrance channel of Wilson Inlet, there is insufficient water movement within the basin to facilitate their subsequent distribution throughout the system. This type of situation must also occur in those numerous southern African estuaries which have similar morphological characteristics (Day *et al.*, 1981).

Acknowledgements

The assistance of G. Hyndes, K. Kershaw, P. Geijsel, D. Gaughan and P. Humphries with sampling is gratefully acknowledged. We also thank R. C. J. Lenanton for his helpful comments on the manuscript. Financial support was provided by the Fisheries Department of Western Australia.

References

Arnott, G. H. & McKinnon, A. D. 1985 Distribution and abundance of eggs of the anchovy, *Engraulis australis antipodum* Gunther, in relation to temperature and salinity in the Gippsland Lakes. *Australian Journal of Marine and Freshwater Research* **36,** 433–439.

Beckley, L. E. 1985 Tidal exchange of ichthyoplankton in the Swartkops estuary mouth, South Africa. *South African Journal of Zoology* **20,** 15–20.

Blackburn, M. 1950 A biological study of the Australian anchovy *Engraulis australis* (White), in Australian waters. *Australian Journal of Marine and Freshwater Research* **1,** 3–84.

Boehlert, G. W. & Mundy, B. C. 1988 Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3,** 51–67.

Claridge, P. N., Potter, I. C. & Hardisty, M. W. 1986 Seasonal changes in movements, abundance, size composition and density of the fish fauna of the Severn Estuary. *Journal of Marine Biology of the Association of U.K.* **66,** 229–258.

Cronin, L. E. & Mansueti, A. J. 1971 The biology of the estuary. In *A Symposium on the Biological Significance of Estuaries* (Douglas, P. A. & Stroud, R. H., eds). Sport Fishing Institute, Washington, D.C., pp. 14–39.

Dando, P. R. 1984 Reproduction in estuarine fish. In *Fish Reproduction Strategies and Tactics* (Potts, G. W. & Wootton, R. J., eds). Academic Press, London, pp. 155–170.

Day, J. H., Blaber, S. J. & Wallace, J. H. 1981 Estuarine fishes. In *Estuarine Ecology with Particular Reference to Southern Africa* (Day, J. H., ed.). Balkema, Rotterdam, pp. 197–221.

Drake, P. & Arias, A. M. 1991 Ichthyoplankton of a shallow coastal inlet in southwest Spain: factors contributing to colonization and retention. *Estuarine, Coastal and Shelf Science* **32,** 347–364.

Fahay, M. P. 1983 Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *Journal of Northwest. Atlantic Fishery Science* **4,** 1–423.

Fortier, L. & Leggett, W. 1982 Fickian transport and the dispersal of fish larvae in estuaries. *Canadian Journal of Fisheries and Aquatic Sciences* **39,** 1150–1163.

Haedrich, R. L. 1983 Estuarine fishes. In *Ecosystems of the World.* Vol. 26: *Estuaries and Enclosed Seas* (Ketchum, B. H., ed.). Elsevier, Oxford, pp. 183–207.

Hodgkin, E. P. & Clark, R. 1988 Estuaries and coastal lagoons of south western Australia. Wilson Inlet, Irwin Inlet and Parry Inlet, estuaries of the Denmark shire. *Environmental Protection Authority, Perth, Western Australia. Estuarine Studies Series No.* **3**.
Hodgkin, E. P. & Di Lollo, V. 1958 The tides of southwestern Australia. *Journal of the Royal Society of Western Australia* **41**, 42–54.
Hutchins, B. & Swainston, R. 1986 *Sea Fishes of Southern Australia. Complete Field Guide for Anglers and Divers*. Swainston Publishing, Perth.
Kinoshita, I. 1986 Postlarvae and juveniles of silver sea bream, *Sparus sarba* occurring in the surf zones of Tosa Bay, Japan. *Japanese Journal of Ichthyology* **33**, 7–12.
Leis, J. M. & Rennis, D. S. 1983 *The Larvae of Indo-Pacific Coral Reef Fishes*. New South Wales University Press, Sydney, and University of Hawii Press, Honolulu.
Leis, J. M. & Trnski, T. 1989 *The Larvae of Indo-Pacific Shorefishes*. New South Wales University Press, Sydney.
Lenanton, R. C. J. 1977 Aspects of the ecology of fish and commercial crustaceans of the Blackwood River estuary, Western Australia. *Fisheries Research Bulletin of Western Australia* **19**, 1–72.
Lenanton, R. C. J. & Hodgkin, E. P. 1985 Life history strategies of fish in some temperate Australian estuaries. In *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration* (Yañez-Arancibia, A., ed.). UNAM Press, Mexico, Chapter 13, pp. 267–284.
Loneragan, N. R., Potter, I. C. & Lenanton, R. C. J. 1989 Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Marine Biology* **103**, 461–470.
Loneragan, N. R. & Potter, I. C. 1990 Factors influencing community structure and distribution of different life-cycle categories of fishes in shallow waters of a large Australian estuary. *Marine Biology* **106**, 25–37.
Miller, J. M., Watson, W. & Leis, J. M. 1979 An atlas of common nearshore marine fish larvae of the Hawaiian islands. *University of Hawaii Sea Grant Program Miscellaneous Report* 80-02.
Miskiewicz, A. G. 1986 The season and length at entry into a temperate Australian estuary of the larvae of *Acanthopagrus australis, Rhabdosargus sarba* and *Chrysophrys auratus* (Teleostei: Sparidae). In *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes* (Uyeno, T., Arai, R., Taniuchi, T. & Matsuura, K., eds). Ichthyological Society of Japan, Tokyo, pp. 740–747.
Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, Jr, A. W. & Richardson, S. L. 1984 *Ontogeny and Systematics of Fishes*. American Society of Ichthyologists and Herpetologists Special Publication No. 1.
Neira, F. J. & Potter, I. C. 1992 The ichthyoplankton of a seasonally closed estuary in temperate Australia: Does an extended period of opening influence species composition? *Journal of Fish Biology*.
Neira, F. J., Potter, I. C. & Bradley, J. S. 1991 Seasonal and spatial changes in the larval fish fauna of a large Australian estuary. *Marine Biology*.
Norcross, B. L. & Shaw, R. F. 1984 Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society* **113**, 153–165.
Okiyama, M. 1988 *An Atlas of the Early Stage Fishes in Japan*. Tokai University Press, Tokyo.
Ozawa, T. 1986 *Studies on the Oceanic Ichthyoplankton in the Western North Pacific*. Kyushu University Press, Fukuoka, Japan.
Pollock, B. R., Weng, H. & Morton, R. M. 1983 The seasonal occurrence of postlarval stages of yellowfin bream, *Acanthopagrus australis* (Gunther), and some factors affecting their movement into an estuary. *Journal of Fish Biology* **22**, 409–415.
Potter, I. C., Beckley, L. E., Whitfield, A. K. & Lenanton, R. C. J. 1990 The roles played by estuaries in the life cycles of fishes in temperate Western Australia and southern Africa. *Environmental Biology of Fishes* **28**, 143–178.
Potter, I. C., Loneragan, N. R., Lenanton, R. C. J., Chrystal, P. J. & Grant, C. J. 1983 Abundance, distribution and age structure of fish populations in a Western Australian estuary. *Journal of Zoology, London* **200**, 21–50.
Roper, D. S. 1986 Occurrence and recruitment of fish larvae in a northern New Zealand estuary. *Estuarine, Coastal and Shelf Science* **22**, 705–717.
Ruple, D. L. 1984 Occurrence of larval fishes in the surf zone of a northern Gulf of Mexico barrier island. *Estuarine, Coastal and Shelf Science* **18**, 191–200.
Russell, F. S. 1976 *The Eggs and Planktonic Stages of British Marine Fishes*. Academic Press, London.
Uchida, K., Imai, S., Mito, S., Fujita, S., Ueno, M., Shojima, Y., Senta, T., Tahuka, M. & Dotsu, Y. 1958 *Studies on the Eggs, Larvae and Juveniles of Japanese Fishes*. Series 1. Second Laboratory of Fisheries Biology, Fisheries Department of the Faculty of Agriculture of the Kyushu University, Fukuoka, Japan [in Japanese].
Weinstein, M. P., Weiss, S. L., Hodson, R. G. & Gerry, L. R. 1980 Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fishery Bulletin* **78**, 419–436.
Whitfield, A. K. 1989*a* Ichthyoplankton in a Southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? *Estuarine, Coastal and Shelf Science* **29**, 533–547.

Whitfield, A. K. 1989*b* Ichthyoplankton interchange in the mouth region of a southern African estuary. *Marine Ecology Progress Series* **54**, 25–33.
Whitfield, A. K. 1990 Life-history styles of fishes in South African estuaries. *Environmental Biology of Fishes* **28**, 295–308.