Estuarine Ichthyoplankton Ecology in Relation to Hydrology and Zooplankton Dynamics in a Salt-wedge Estuary

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Abstract. The ichthyoplankton assemblage of the Hopkins River estuary, Victoria, was dominated by estuarine taxa that included demersal (goby, gudgeon) and pelagic (black bream, estuary perch, anchovy) species. The two seasonal peaks in fish larvae abundance were related to (1) the spring/summer zooplankton increase that occurred after flooding of the estuary and was comprised predominantly of copepod nauplii, thereby providing a good prey field for very young fish larvae, and (2) the autumn zooplankton maxima, which would provide a wide selection of copepod stages and meroplankton and promote dietary partitioning and flexibility among older larval stages. The two peaks in fish larvae abundance occurred well before and well after the attainment of maximum water temperature in the estuary. Goby, gudgeon, estuary perch and anchovy larvae were in the plankton over an extended period coinciding with the more stable conditions of salt-wedge presence and maximum zooplankton densities. The spawning of black bream and anchovies in the estuary was clearly related to physical conditions, such as salinity and water temperature, and habitat—although spawning of both species also occurred at times of high concentrations of potential prey organisms for their larvae. Adults of all the above fish species appear to have evolved spawning strategies that are adapted to the average hydrological and biological conditions in the estuary that would lead to the enhanced survival of their larvae. With the exception of the black bream, it appears that a ubiquitous and prolonged rather than a synchronous and confined spawning strategy is more widely used by estuarine-spawning fishes in the Hopkins River estuary. This type of spawning strategy, combined with the generally high density of food available to fish larvae in estuaries, suggests that the match–mismatch hypothesis of Cushing may be less relevant in the estuarine than in the marine environment.

Introduction

Many Australian fish species of commercial and recreational importance depend on estuaries during at least one stage of their life history (Pollard 1981; Lenanton and Potter 1987; Blaber *et al.* 1989). The site of the present study, the Hopkins River estuary, supports an important recreational fishery for black bream, *Acanthopagrus butcheri*, and estuary perch, *Macquaria colonorum* (Tunbridge and Glenane 1985), and both these species spawn in the estuary.

Although fish spawning and larval recruitment in the marine environment have been shown to be closely related to water temperature, photoperiod and seasonal plankton production (e.g. Royce 1972; Cushing 1975; Bye 1984; Sherman *et al.* 1984; Allen and Barker 1990), only a few studies have investigated ecological relationships between estuarine-spawned larval fishes and both hydrodynamics and plankton cycles in estuaries. These few studies have found that peak spawning for some species is in synchrony with seasonal increases in abundance of their dominant copepod prey (Sherman *et al.* 1984; Townsend 1984), with maximum catch rates of dominant larval fishes closely coupled to zooplankton dynamics. For example, the 'match– mismatch'

hypothesis of Cushing (1975, 1990) proposes that the spawning of marine fish should be timed such that the appearance of larvae overlaps with seasonal plankton blooms. Conversely, other species have developed a ubiquitous spawning strategy, producing larvae over a protracted period, thus allowing these populations to increase rapidly in response to favourable conditions and prey that are temporally restricted (Sherman *et al.* 1984).

The present study examined the composition and relative abundance of fish larvae and eggs along the entire length of the Hopkins River estuary to determine changes in temporal and spatial abundances. Comparisons were made between the distributions of ichthyoplankton, hydrological parameters and the remaining zooplankton community to assess possible relationships. Potential links between the spawning patterns of adult fishes and the annual hydrological cycle were inferred from ichthyoplankton ecology.

Materials and Methods

Study Site

The Hopkins River estuary is a truncated salt-wedge type situated on the south-western coast of Victoria, near Warrnambool (Fig. 1). The estuary is characterized by low tidal energy (the semi-diel tides have a maximum
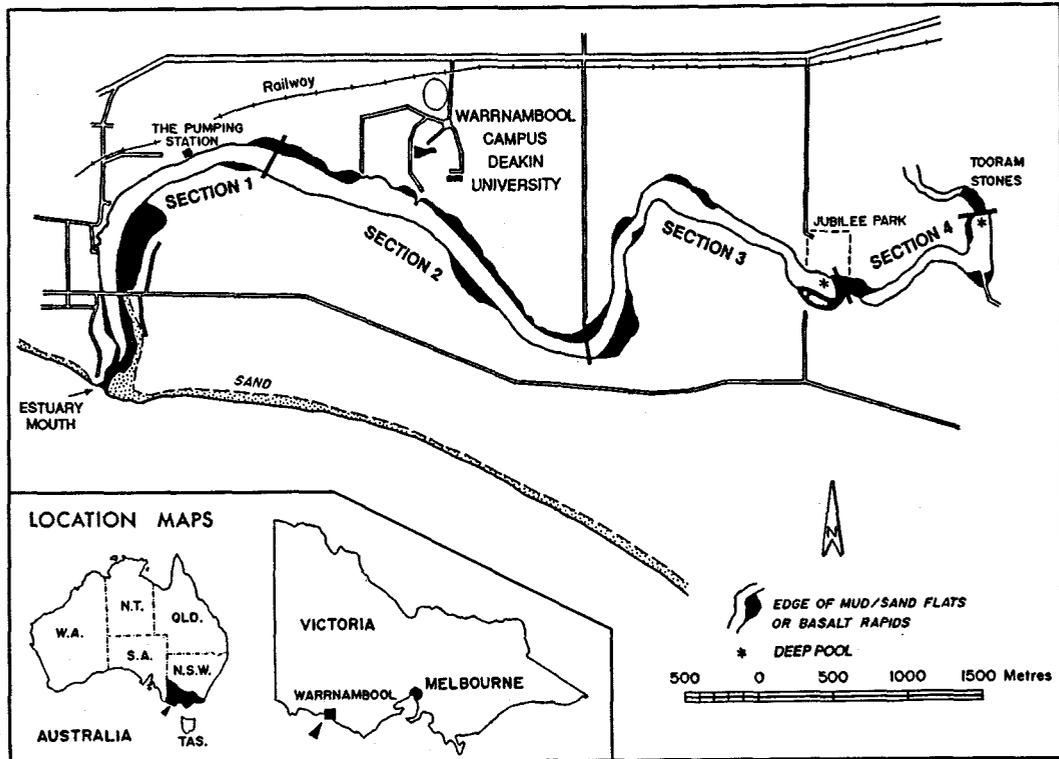
Fig. 1. Hopkins River estuary. The four estuary sections used for the sampling surveys are also indicated.

range of about 1 m) and drains into the Southern Ocean. It consists of a single discrete and well defined channel of 9·2 km length and has an average width 164 m. The upstream limit of tidal movement is clearly defined by a natural dam of lava that crosses the course of the river at Tooram Stones (Gill 1981). Another lava crossing occurs near Jubilee Park (~7 km from the estuary mouth) and is about 1 m below the normal water height (Sherwood and Backhouse 1982). Deep pools have formed on the downstream side of these lava crossings; the Tooram Stones pool has a depth of 13 m and the Jubilee Park pool has a depth of 11 m (Fig. 2). The estuary is generally shallow elsewhere (Fig. 2). The mouth of the Hopkins River estuary has a calcarenite sill that contributes to the formation of a sand bar (Gill 1977); the extent of the bar depends on longshore sand drift, winds and river discharge. The hydrodynamics of the estuary are influenced by the sill and sand bar, particularly in terms of water exchange at the mouth, although complete closure is uncommon.

For sampling purposes the estuary was divided into four longitudinal strata based on gross channel morphology and bottom topography such that the internal physiography of each stratum was more homogeneous than the estuary overall. These strata are referred to in the paper as Sections 1, 2, 3 and 4, with Section 1 being the most downstream section and Section 4 the most upstream (Figs 1 and 2).

Annual Hydrological Cycle

The annual hydrological cycle of the Hopkins River estuary can be characterized by two main periods of river discharge as determined by rainfall, i.e. high flow and low flow, and three phases of salt-wedge dynamics, i.e. reduction/absence, emplacement and presence (Newton 1994). These phases and the main physico-chemical features associated with them are summarized by the model shown in Fig. 3. During high flow, from late winter to early spring, river discharge peaks and the estuary is usually flushed of saline waters during high-velocity floods; water

temperature is at a minimum at this time. During low flow, from late spring to early winter, a new salt-wedge is reformed along the estuary and subsequently stagnates during the highly stratified conditions of salt-wedge presence. This period is characterized by higher salinities and water temperatures, with highest values generally occurring in late summer.
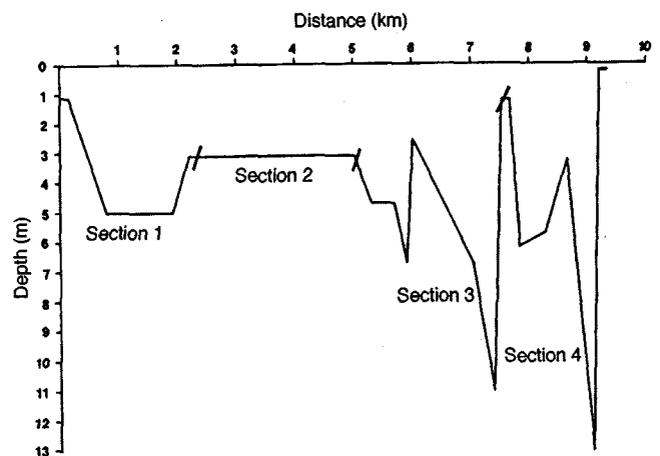

Fig. 2. Depth profile of the Hopkins River estuary and distance to upstream tidal limit. This highlights the deep pools of Jubilee Park (11 m deep and ~7 km from estuary mouth) and Tooram Stones (13 m deep and at tidal limit of estuary). The four estuary sections used for the sampling surveys are also indicated.
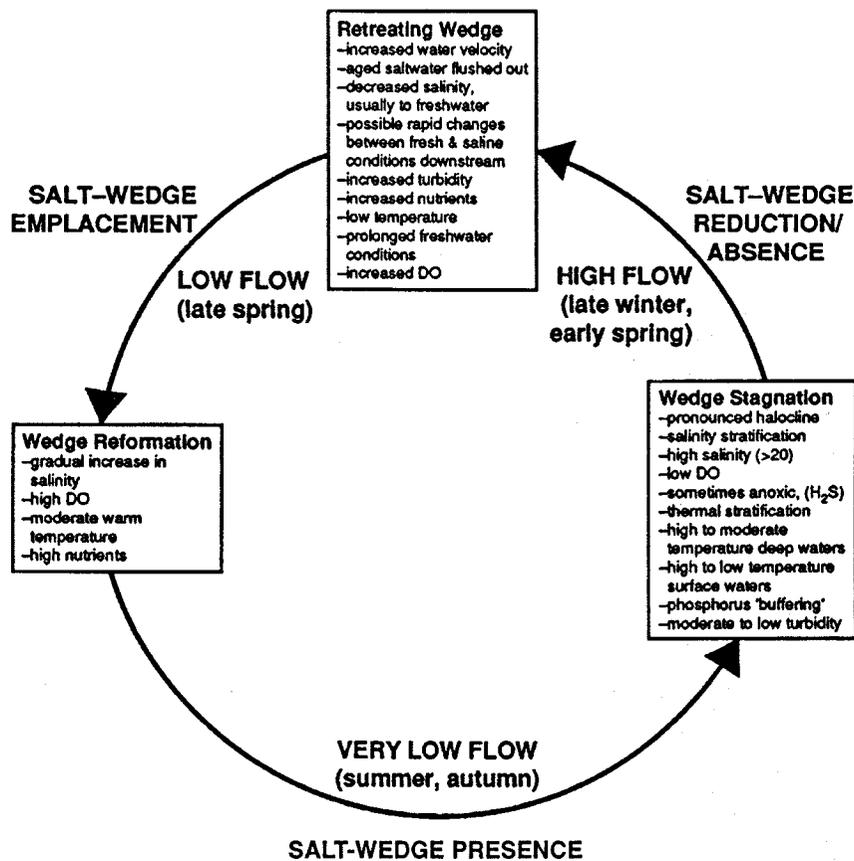
SALT-WEDGE EMPLACEMENT

LOW FLOW (late spring)

Retreating Wedge
-increased water velocity
-aged saltwater flushed out
-decreased salinity, usually to freshwater
-possible rapid changes between fresh & saline conditions downstream
-increased turbidity
-increased nutrients
-low temperature
-prolonged freshwater conditions
-increased DO

SALT-WEDGE REDUCTION/ ABSENCE

HIGH FLOW (late winter, early spring)

Wedge Reformation
-gradual increase in salinity
-high DO
-moderate warm temperature
-high nutrients

Wedge Stagnation
-pronounced halocline
-salinity stratification
-high salinity (>20)
-low DO
-sometimes anoxic, (H₂S)
-thermal stratification
-high to moderate temperature deep waters
-high to low temperature surface waters
-phosphorus 'buffering'
-moderate to low turbidity

VERY LOW FLOW (summer, autumn)

SALT-WEDGE PRESENCE

Fig. 3. Model of the annual hydrological cycle of the Hopkins River estuary (modified from Sherwood 1985) and the three phases of salt-wedge dynamics (Newton 1994) . DO, dissolved oxygen.

Sampling

Zooplankton sampling (including the capture of fish eggs and larvae) and measurement of physico-chemical conditions were carried out over a 20-month survey period from July 1983 to February 1985. Zooplankton samples were collected during daylight with a 24·4-L Schindler-type zooplankton trap with an outlet mesh size of 80 μm. Zooplankton was collected according to a stratified random design (Elliot 1977), at the surface and at a depth of 2–4 m, at three randomly selected stations in each of the four estuary sections; stations were selected randomly each month from a grided map and a table of random numbers (after Elliot 1977). In addition, the deep pools of Jubilee Park and Tooram Stones were routinely sampled. Profiles of salinity, temperature and dissolved oxygen were measured at each station; salinity values are quoted according to the Practical Salinity Scale of 1978 (PSS 78). For the last 13 months of the survey period (i.e. February 1984 to February 1985), fish eggs and larvae were also sampled with a 0·5-m-diameter, 250-μm-mesh conical net equipped with a flow-meter; this type of sampling gear is more typical of ichthyoplankton studies. Oblique tows (from near-bottom to the surface) were made during daylight at two of the stations selected for zooplankton trap sampling, in each of the four estuary sections. Tows were of about 3 min duration and filtered between 10 and 20 m³ of water. All plankton samples were preserved with 5% formaldehyde.

Counts of zooplankton trap samples were converted to no. m⁻³ for fish eggs and larvae and other zooplankton types (most notably calanoid copepods and nauplii, and medusae). Ichthyoplankton data from the zooplankton trap samples are used in this paper for comparison with abiotic data owing to their closer proximity on collection; other ichthyoplankton results discussed are from the analysis of net samples. Ichthyoplankters from the net samples were either counted in entirety or subsampled with a 'Kahlisco' Folsom-type splitter. Concentrations (no. m⁻³) of fish larvae and fish eggs were determined from the net samples; means refer to the mean value of the two or three stations per estuary section or the mean for the whole estuary, maxima refer to the highest value for an individual sample. The term fish 'larva' used in this paper includes the yolk-sac, preflexion, flexion and postflexion stages as described by Leis and Trnski (1989). Most larvae of black bream and estuary perch in the samples were newly hatched yolk-sac and preflexion larvae, and it proved difficult to separate them during routine counting; these larvae are referred to as the black bream/estuary perch group. For routine analysis, goby and gudgeon larvae were also counted as a group, with quantitative assessments of individual species made at the time of their peak abundance only. Eggs of the black bream were distinguished from those of estuary perch on the basis of their smaller size and the description of Munro (1944); black bream eggs had a diameter of 0·6 to 0·75 mm ($n = 10$), and estuary perch eggs had a diameter of 0·93 to 1·05 mm ($n = 10$). Southern anchovy eggs were easily identified by their elliptical rather than spherical shape. Gobies and gudgeons typically have demersal eggs (Cadwallader and Backhouse 1983), so these eggs would not occur in the plankton samples.

Results

Composition, Concentration and Distribution of the Ichthyoplankton Assemblage

In all, 69 883 fish larvae, representing 9 families and 11 species, were collected in the Hopkins River estuary over the 13-month net survey (Table 1). Most of the species found were spawned in the estuary: three species of goby (*Afureagobius tamarensis*, *Arenigobius bifrenatus* and *Pseudogobius olorum*), a gudgeon (*Philypnodon grandiceps*), southern anchovy (*Engraulis australis*), black bream (*Acanthopagrus butcheri*) and estuary perch (*Macquaria colonorum*). Larvae of the families Tripterygiidae, Clinidae, Tetraodontidae and Atherinidae were rarely encountered (<5 individuals). The most common larvae were those of the goby/gudgeon assemblage, which represented over 70% of the total number of fish larvae. The black bream/estuary perch larval group contributed nearly 30%. However, it is likely that larvae of black bream made up the bulk of this group because 94·5% of fish eggs found were those of the black bream. Eggs belonging to three species—black bream, estuary perch and southern anchovy—were identified.

Both the trap and net methods of sampling produced similar results of ichthyoplankton presence and abundance along the estuary (e.g. Fig. 4). Analysis of zooplankton trap samples showed that fish larvae were rarely located in the surface water layer of the estuary, suggesting that they occurred mainly below the halocline in the deeper salt-wedge layer of the estuary (Table 2). Goby/gudgeon larvae

dominated all estuary sections, with the exception of Section 3 where bream/perch larvae were most abundant (Table 3).

Seasonal peaks in concentrations of fish larvae were comprised of goby and gudgeon larvae, apart from the November post-flood period in the upper estuary (Fig. 4). *A. bifrenatus* larvae dominated the goby/gudgeon group downstream in early autumn (maxima 298 m^{-3} in April in Section 1; Fig. 4*a*). However, overall the most common species of the goby/gudgeon group was the larvae of the gudgeon *P. grandiceps*. This species showed two main seasonal peaks in abundance—late summer and winter—possibly implying two spawning periods. Mean concentration peaked in May 1984 (166 m^{-3}) and February 1985 (117 m^{-3}) in Section 2 (Fig. 4*b*). *P. grandiceps* was the only fish collected as larvae throughout the estuary over winter. Peak concentrations for the goby larvae *P. olorum* and *A. tamarensis* were comparatively small. Larvae of *P. olorum* peaked in January 1985 (28 m^{-3} to 38 m^{-3}), mainly in mid to upstream estuary sections (Figs 4*b*–4*d*) and larvae of *A. tamarensis* peaked in February (5 m^{-3} to 10 m^{-3}), mainly in downstream sections (Figs 4*a* and 4*b*). As a group, goby/gudgeon larvae were least abundant in the

Table 1. Larval fish fauna of the Hopkins River estuary, taken in plankton samples between February 1984 and February 1985
E indicates that adults of the species are known to spawn in estuaries, M indicates that adults are most likely marine spawners and the larvae are marine stragglers, * refers to those species for which fish eggs were identified

Taxon	Common name	Spawning habitat
Atherinidae	Hardyhead	E
Clinidae	Weedfish	M
Eleotridae		
Philypnodon grandiceps	Flat-headed gudgeon	E
Engraulididae		
Engraulis australis	Southern anchovy*	E
Gobiidae		
Afureagobius tamarensis	Tamar River goby	E
Arenigobius bifrenatus	Bridled goby	E
Pseudogobius olorum	Blue-spot goby	E
Percichthyidae		
Macquaria colonorum	Estuary perch*	E
Sparidae		
Acanthopagrus butcheri	Black bream*	E
Tetraodontidae	Toadfish	E
Tripterygiidae	Triplefin	M

Table 2. Percentage mean concentrations of fish larvae (no. m^{-3}) and eggs (no. m^{-3}) in surface and depth (2–4 m) water layers in each of the four estuary sections over the 20-month zooplankton trap survey

	Section			
	1	2	3	4
Fish larvae				
Surface	8	5	2	0
Depth	92	95	98	100
Fish eggs				
Surface	0	0	0	17
Depth	100	0	100	83

Table 3. Mean concentration of fish larvae (no. m^{-3}) and eggs (no. m^{-3}) in each estuary section and for the Hopkins River estuary as a whole, from the 13-month net survey
T, total

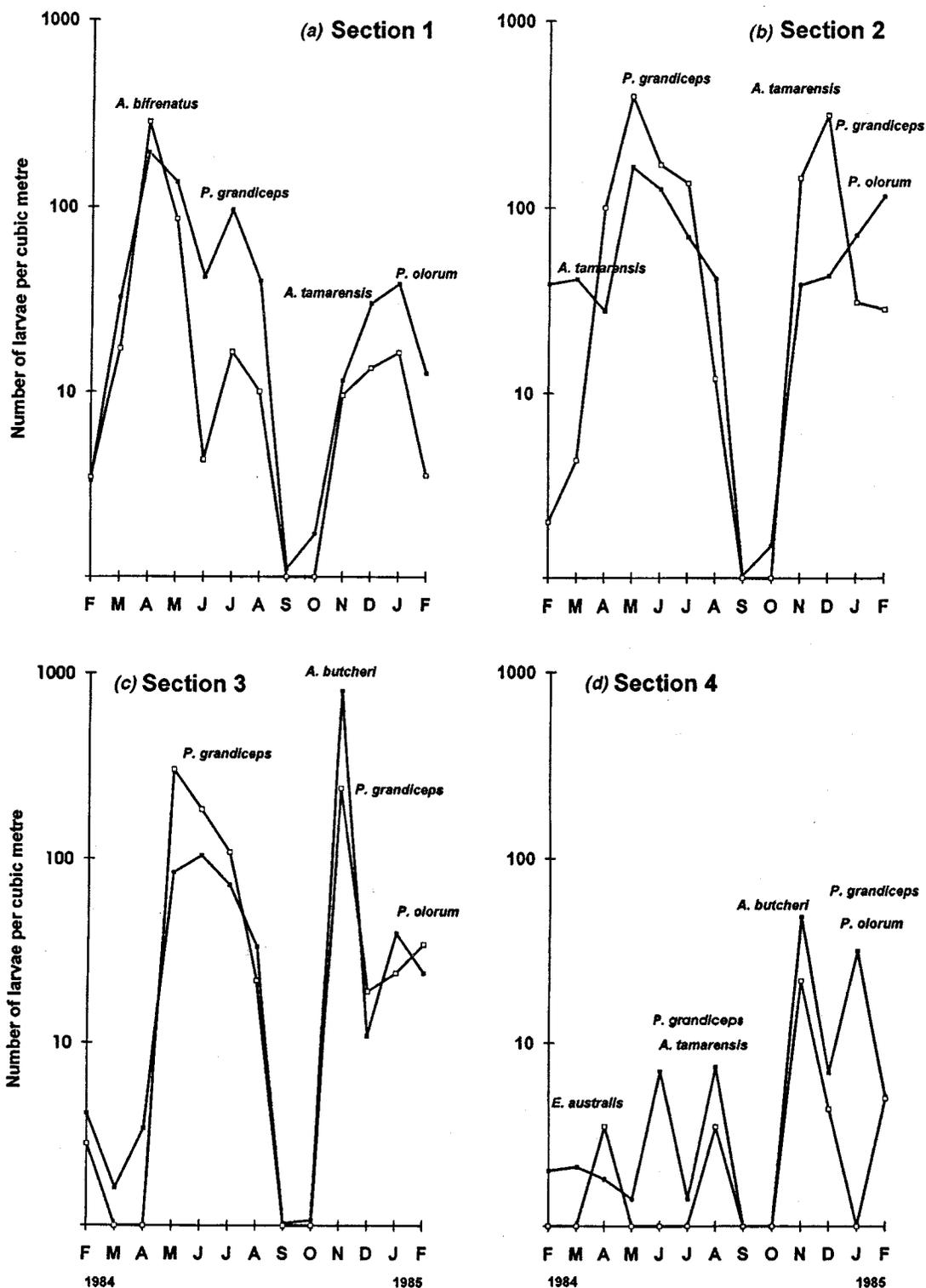|	Section				Estuary
	1	2	3	4	
Fish larvae (T)	48·4	59·5	90·3	8·0	51·5
Goby/gudgeon	48·4	59·4	30·2	6·8	36·2
Bream/perch	0·0	0·1	60·0	1·1	15·3
Anchovy	0·01	0·02	0·12	0·07	0·06
Fish eggs (T)	0·4	1·6	48·5	5·2	14·0
Black bream eggs	0·2	1·2	46·9	4·4	13·2
Estuary perch eggs	0·1	0·4	1·6	0·0	0·5
Anchovy eggs	0·0	0·05	0·1	0·8	0·2

Fig. 4. Mean monthly concentration (no. m^{-3}) of fish larvae, from February 1984 to February 1985, in the Hopkins River estuary. *(a)* Section 1, *(b)* Section 2, *(c)* Section 3, *(d)* Section 4. Mean concentrations are given for (■) net samples and (□) zooplankton trap samples from the deep water layer (2–4 m). As deduced from qualitative assessments, dominant contributions of the various fish larvae species to various abundance peaks are indicated on the figures. Species are: *Afureagobius tamarensis*—Tamar River goby; *Arenigobius bifrenatus*—bridled goby; *Pseudogobius olorum*—blue-spot goby; *Philypnodon grandiceps*—flat-headed gudgeon; *Acanthopagrus butcheri*—black bream; *Engraulis australis*—southern anchovy.

upper estuary of Section 4 (generally <30 m^{-3}; Fig. 4d), being most prevalent in mid to downstream sections of the estuary.

The highest concentration of fish larvae was recorded at the Jubilee Park deep pool (Section 3) in November 1984 (mean 806 m^{-3}, maxima 1546 m^{-3}) and consisted mainly of the newly hatched yolk-sac larvae of black bream and estuary perch (Fig. 4c). Only a few postflexion stages of black bream and estuary perch larvae were caught, the latest being in February 1985. Anchovy larvae were present over late summer and autumn, mainly in upstream estuary sections (Table 3). Concentrations were generally less than 1 m^{-3}, with a maximum of 1·1 m^{-3} recorded in February 1984 in Section 4 (Fig. 4d).

Analysis of zooplankton trap samples revealed that fish eggs were rarely found in the surface waters of the estuary (Table 2). The presence of bream eggs was restricted to the post-flood period of salt-wedge emplacement, between November and January (Fig. 5a); a similar result was found in both 1983 and 1984. Conversely, estuary perch eggs were collected over winter (June to August), prior to the flood, as well as in the post-flood period of November to January (Fig. 5b). The concentration of fish eggs peaked in November 1984, mainly at the Jubilee Park deep pool in Section 3 (Table 3, Figs 5a and 5b). Of these eggs, 96% were those of the black bream and 4% were the larger estuary perch eggs. Maxima of 1077 m^{-3} were recorded for black bream eggs and 21.6 m^{-3} for estuary perch eggs. A smaller peak of black bream eggs (57 m^{-3}) occurred in

December 1984, mainly at the Tooram Stones deep pool (Fig. 5a). Anchovy eggs were found over late summer and autumn, and the highest mean concentration of 5.4 m^{-3} was recorded in Section 4 in February 1984 (Table 3, Fig. 5c).

Abiotic Factors and Ichthyoplankton Distribution

Over the 20-month survey, salinities in the estuary ranged from freshwater conditions to 35. Surface salinities were consistently lower than those of the deeper salt-wedge layer (Fig. 6a), and overall they were lowest in Section 4 at the head of the estuary. Scouring floods occurred in September of 1983 and 1984 that rendered the estuary fresh for one to three months, with the longest periods of fresh water in upstream sections. After flooding, a new salt-wedge reformed along the estuary and the water column became highly stratified over the summer to winter period. Salinities of the wedge were generally above 30 at this time. Water temperature ranged from 7·3°C to 26·3°C, with lowest temperatures over July to September and highest temperatures over January to February. Surface waters were warmer than the wedge layer in summer, whereas the wedge layer was warmer than the surface in winter (Fig. 6b).

Relatively high concentrations of dissolved oxygen (6–13 mg O_2 L^{-1}) were recorded throughout most of the estuary over the study period, particularly in waters of less than 4 m depth. However, during the highly stratified conditions of salt-wedge presence, the deeper saline waters gradually became depleted of oxygen. During this phase of salt-wedge dynamics, persistently low dissolved oxygen
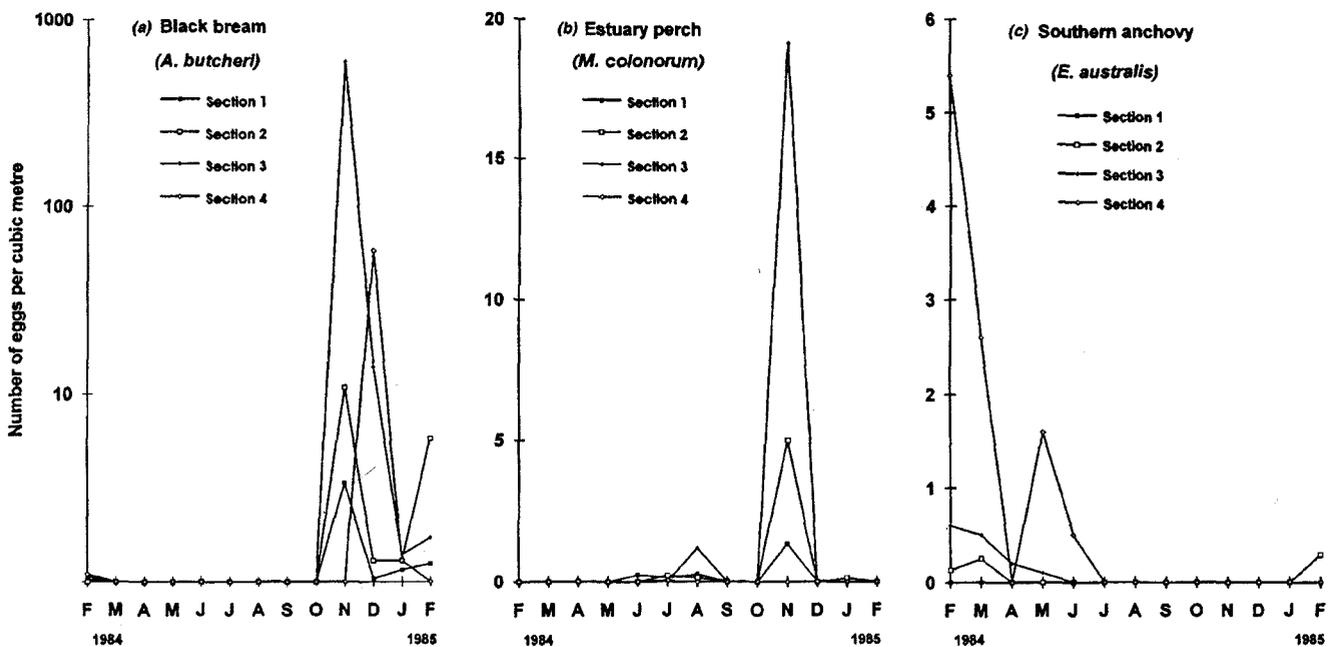

Fig. 5.   Mean monthly concentration (no. m^{-3}) of fish eggs, from February 1984 to February 1985, for the pelagic fishes (a) A. butcheri, (b) M. colonorum and (c) E. australis, in the four estuary sections. Note the different scales on the y-axis for each species.
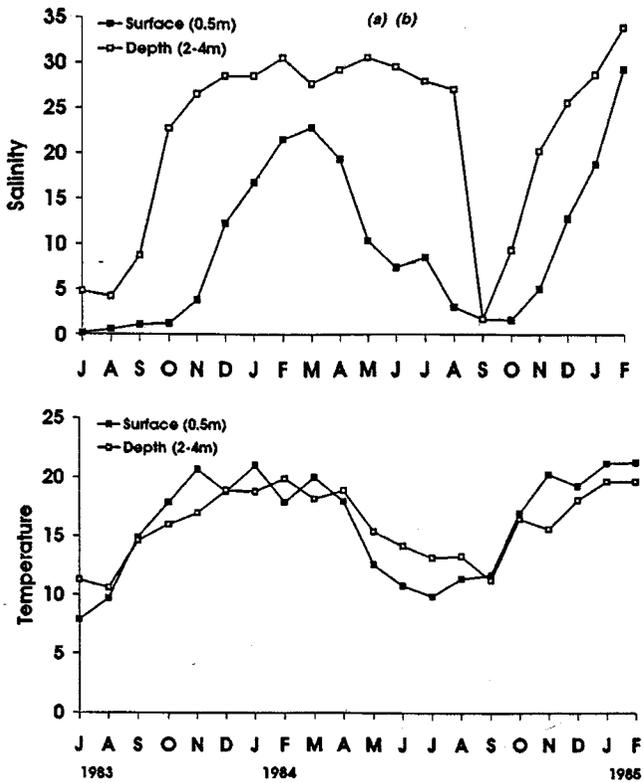
Fig. 6. Physico-chemical measurements from the Hopkins River estuary. (a) Mean monthly salinity for the surface water layer and at a depth of 2 to 4 m. (b) Mean monthly water temperature (°C) for the surface water layer and at a depth of 2 to 4 m.

concentrations of <1–2 mg O_2 L^{-1} occurred at depths of >4 m along the estuary. This was typical of waters in the deep pools at Jubilee Park and Tooram Stones, particularly from summer to winter (Newton 1994).

Ichthyoplankton data from the zooplankton trap samples showed that fish larvae and eggs were distributed over a wide range of salinities and water temperatures. Fish larvae were found in salinities ranging from 2·8 to 34 and temperatures of 9·3°C to 23·1°C. Fish eggs were found in salinities ranging from 2·1 to 30·5 and temperatures of 14·9°C to 23·1°C. However, most fish larvae were taken in salinities greater than 27.5 (almost 50% of total mean concentration, Fig. 7b) and in moderate temperatures of 12·6°C to 17·5°C (about 75% of total mean concentration, Fig. 7d). The majority of fish eggs were taken from a narrower temperature range, 14·9°C to 17·5°C (almost 75% of total mean concentration, Fig.7c), and from the moderate salinity range of 17·6 to 22·5 (about 70% of total mean concentration, Fig. 7a).

The peak concentrations of black bream eggs occurred in the two deep pools, but one month apart. In November, sub-halocline salinities of 20 to 25 and water temperatures of 15.5°C occurred in the Jubilee Park deep pool, whereas in the Tooram Stones deep pool salinities of about 13 and temperatures of about 17°C prevailed. In December, salinities of 25 to 28 and 21 to 22 occurred at each site, respectively. The majority of anchovy eggs were found in February and March in Section 4, where water temperatures
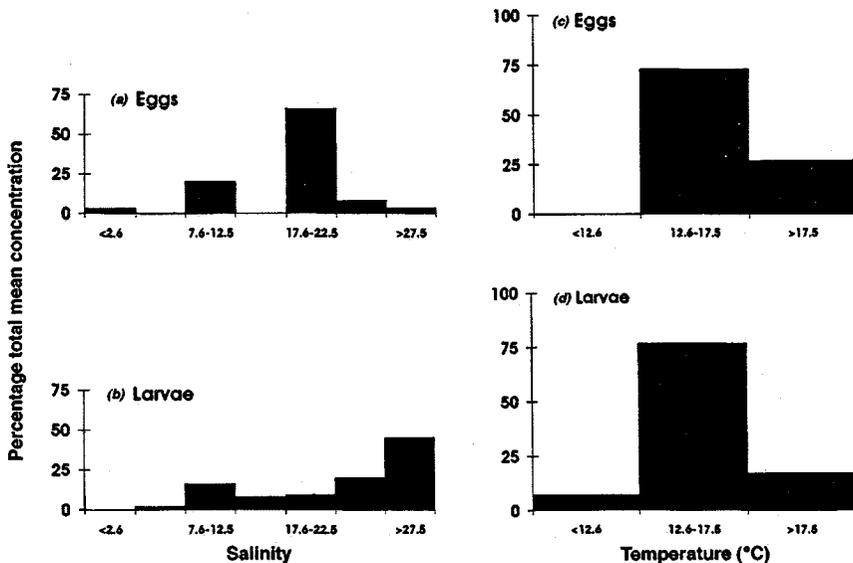

Fig. 7. Percentage mean concentration (no. m^{-3}) of fish larvae and eggs (i.e. from zooplankton trap samples taken from July 1983 to February 1985) over several ranges of salinity and water temperature. (a) Fish eggs —salinity ranges. (b) Fish eggs—temperature ranges. (c) Fish larvae—salinity ranges. (d) Fish larvae—temperature ranges.

were 18°C to 23°C (mainly 19°C to 20°C) and sub-halocline salinities were 25 to 32 (mainly 28). In both months, salinities were generally higher (i.e. >30) in downstream sections and water temperatures were 2°C to 3°C cooler.

Zooplankton and Ichthyoplankton Distribution

Comparison of ichthyoplankton and zooplankton data showed a pattern of peaks in abundance of fish larvae occurring one to two months after the peaks in total zooplankton and calanoid nauplii abundances that were greater than 10^5 m^{-3} (Fig. 8), a pattern that was repeated in all four estuary sections (Newton 1994). This pattern related to the peaks due to larvae of the goby/gudgeon group. Although not shown here, there was a similar synchrony between density peaks of these fish larvae and density peaks of the dominant zooplankter, the calanoid copepod *Gippslandia estuarina*, at greater than 10^5 m^{-3} (Newton 1994). This pattern was followed by a decline in abundance by all groups over winter months. The peak of fish larvae in November (due mainly to black bream larvae) was in synchrony with the ascending limb of the late-summer/early-autumn zooplankton curve. At that time calanoid nauplii would be the main prey available to fish

1000000 ⊤

100000 ⊤

10000 ⊤

1000 ⊤

100 ⊤

10 ⊤

Mean number per cubic metre

F   M   A   M   J   J   A   S   O   N   D   J   F
1984   1985

Fig. 8. Mean concentration (no. m^{-3}), for the Hopkins River estuary from February 1984 to February 1985, of (■) total zooplankton (including fish larvae), (▲) calanoid nauplii, and (●) the medusa *Australomedusa baylii* sampled by the zooplankton trap (80-μm mesh) in the deep water layer (2–4 m), and (◇) mean concentration (no. m^{-3}) of fish larvae sampled by the net (250-μm mesh).

larvae. However, the prey available to fish larvae was consistently abundant throughout the year, apart from in the flood period. The medusa *Australomedusa baylii* was observed on several occasions to have ingested fish larvae and fish eggs from the Hopkins River estuary (Newton 1994). Peak densities of medusae occurred over summer (Fig. 8).

Discussion

Ichthyoplankton Assemblage

Only 11 species of fish larvae were found in the Hopkins River estuary, of which only seven were common. This is low considering that about 60 fish species have been recorded from the estuary (B. Mitchell, unpublished, Deakin University). Fish eggs belonging to only three species were identified. Low species richness in larval fish assemblages has often been reported in other riverine estuaries (e.g. Melville-Smith and Baird 1980; de Lafontaine et al. 1984; Neira and Potter 1992, 1994; Neira et al. 1992). In the lower Swan River estuary, Western Australia, only two of the several marine fish species found in abundance in the estuary were caught as larvae, which implies that the other abundant marine fish enter the estuary as juveniles (Gaughan et al. 1990). A similar situation could occur in the Hopkins River estuary.

Species richness of fish larvae was similar along the entire length of the Hopkins River estuary. In contrast, species richness of fish larvae is generally highest in the lower regions of estuaries close to the sea, as occurs in Lake Macquarie (Miskiewicz 1987) and the Swan River estuary (Gaughan et al. 1990; Neira et al. 1992). This is due to the higher incidence of marine species that enter the lower reaches of estuaries (Lenanton and Potter 1987; Gaughan et al. 1990; Neira et al. 1992; Neira and Potter 1994). The mid to upper reaches of estuaries are generally dominated by estuarine-spawned larvae (e.g. Neira et al. 1992).

The ichthyoplankton assemblage of the Hopkins River estuary was dominated by estuarine-spawned species, and the incidence of marine-spawned species was extremely low. It is likely that the low degree of tidal exchange and the sill at the estuary mouth contribute to this phenomenon and limit the entry of marine fish larvae into the estuary. Marine teleosts that enter estuaries as larvae typically rely on tidal transport through unobstructed estuary mouths for their upstream migration (Miskiewicz 1987). Similarly, in the Swan River estuary, another salt-wedge estuary with a sill, the larvae of the 13 teleosts that spawn within the estuary contributed about 94% to the total catch (Neira et al. 1992). The type of ichthyoplankton found in the Hopkins River estuary conforms with the general composition of the zooplankton, which consisted almost exclusively of true estuarine species, with no established marine component (Newton 1994).
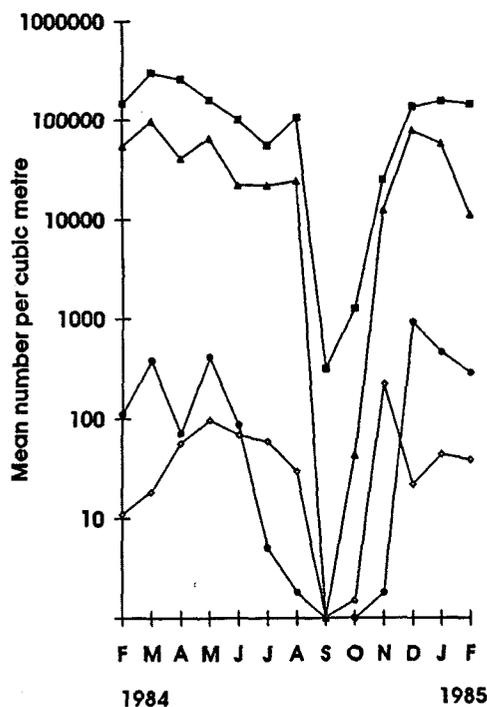
The goby/gudgeon larval complex dominated the ichthyoplankton assemblage of the Hopkins River estuary and comprised over 70% of the total catch. Similarly, the assemblage in the Swan River estuary and Wilson Inlet, WA, was found to be dominated by gobies (Neira and Potter 1992; Neira et al. 1992). Dominance by gobiid larvae is typical of the larval fish assemblages of many temperate estuaries and marine embayments elsewhere (e.g. Houde and Alpern Lovdal 1984; Beckley 1986; Steffe 1991).

Most fish larvae caught in this study were at the preflexion and flexion stages of development, with postflexion larvae being relatively rare. This is a common occurrence in estuarine ichthyoplankton (Drake and Arias 1991). Larval stages of estuarine fishes are often stratified within the water column and many species are often more abundant near the bottom (Weinstein et al. 1980; Allen and Barker 1990; Steffe 1991). In addition, older larval stages may show diel vertical migratory behaviour, e.g. gobies (Miskiewicz 1987), which may minimize their capture by daylight sampling as used in the present study. Despite this, comparisons of ichthyoplankton abundance from other Australian and overseas estuaries suggest that the abundance of larval fishes in the Hopkins River estuary is comparatively high (Table 4).

Seasonal and Spatial Trends of Ichthyoplankton

The concentration of fish larvae in the Hopkins River estuary followed a seasonal trend in which the two main peaks in abundance were comprised of different species groups. The well defined late-spring ichthyoplankton peak was due to larvae spawned from black bream and estuary perch. The more protracted ichthyoplankton peak of mid autumn to mid winter was comprised of larvae from the goby/gudgeon group. Such protracted spawning periods are typical of many gobiid species throughout the world (Darcy 1980; Neira et al. 1992). Spring/summer and autumn peaks in the concentration of fish larvae have been reported from other Australian estuaries (e.g. Kott 1955; Hodgson 1979; Miskiewicz 1987; Gaughan et al. 1990; Neira et al. 1992; Neira and Potter 1994).

In the Swan River estuary, the highest concentration of fish larvae occurred two to four months before the attainment of maximum mean monthly water temperature (Neira et al. 1992). This situation also parallels that found in other temperate estuaries and marine embayments (Steffe and Pease 1988; Gaughan et al. 1990). A similar situation occurred in the Hopkins River estuary, with the peak of fish larvae abundance in late spring occurring three months before the maximum monthly water temperature and the autumn peak occurring about three months afterwards. Moderate temperature is often an important requirement of spawning, egg incubation time, and larval fish growth (Hunter 1981; Gaughan et al. 1990).

It appears that both fish eggs and fish larvae occur almost exclusively in the deeper salt-wedge layer of this stratified estuary. Therefore, the halocline may act as a barrier, inhibiting the eggs and larvae from entering the upper seaward-flowing surface water layer and being lost from the system. In addition, fish eggs were mainly restricted to the two upstream sections. This would further assist their retention in the estuary owing to both the increased distance from the mouth and the presence of deeper waters.

Table 4. Ichthyoplankton concentrations (no. m^{-3}) reported from estuaries

For the present study and that of the Barwon complex, sampling method—i.e. trap (80-μm mesh) or net (250-μm mesh)—is indicated. *, mean from trap samples was calculated from the same 13-month period as the net sampling and only from the samples from the deep water layer

Estuary	Fish larvae	Fish eggs	Comment	Reference
Australia				
Hopkins River	2791	1149	Max. (trap)	Present study
	1546	1093	Max. (net)	Present study
	53·2	14	Mean (trap)*	Present study
	51·5	—	Mean (net)	Present study
Barwon complex	2791		Max. (trap) Gobiidae	Sherwood et al. (1987)
Gippsland Lakes	90·1	0·1 to 382	Max.; range anchovy eggs	Arnott and McKinnon (1985)
Tuggerah Lakes	7		Mean of larvae and eggs	Hodgson (1979)
Lake Macquarie	8·5		Mean of larvae and eggs	Hodgson (1979)
Swan River	3·1	—	Maximum	Neira et al. (1992)
Lower	0·42		Mean	Neira et al. (1992)
Upper	1·97	—	Mean	Neira et al. (1992)
Lower Swan River	2·0	60·3	Mean maxima	Gaughan et al. (1990)
South Africa				
Swartkops River	1·3		Mean Gobiidae	Melville-Smith and Baird (1980)
Kromme River	41·8		Maximum	Melville-Smith (1981)

Timing of Fish Spawning and Estuarine Hydrodynamics

As indicated by the first appearance of larvae in the plankton, adults of the flat-headed gudgeon, Tamar River goby, black bream and estuary perch spawn first in early spring, with the blue-spot goby and bridled goby spawning next in early summer and anchovy spawning last in late summer. These spawnings coincide with the two phases of post-flood salt-wedge dynamics, i.e. emplacement and presence (Newton 1994; see Fig. 3). In addition, estuary perch also spawned before the flood in mid to late winter, as did adults of the gudgeon larvae.

Results of this study suggest that the black bream is a synchronous spawner, with spawning taking place over a relatively restricted time and place. Conversely, they suggest that the gobies, gudgeon, estuary perch and anchovy are ubiquitous spawners, spawning over a protracted period of more than five months. The timing and duration of spawning for these species, as inferred from ichthyoplankton distributions, suggest a combination of spawning and egg hatching times that would ensure a succession in the occurrence of larvae through time. It has often been reported that estuarine fish have extended spawning seasons to act as a 'buffer' against failure of recruitment as a result of droughts or unseasonable floods or to ensure the synchrony of at least some larvae with blooms of planktonic food organisms (Melville-Smith and Baird 1980; Townsend 1983). Extended larval presence in the plankton may also be achieved by variable egg hatching times within the clumps of demersal eggs typically laid by species such as gobies and gudgeons (Townsend 1983). Such strategies would also reduce competitive interactions between the different larval types in the plankton (de Lafontaine et al. 1984).

Spawning periods for the seven common estuarine-spawning fishes from the Hopkins River estuary are within the reported ranges from other estuarine environments (Cadwallader and Backhouse 1983; Hobday and Moran 1983; Arnott and McKinnon 1985; Neira and Potter 1992; Neira et al. 1992). Of these species, only the southern anchovy and blue-spot goby are known to spawn in both the marine and estuarine environments (Miskiewicz 1987; Gaughan et al. 1990). The use by anchovies of estuarine environments as nursery habitats is well documented in both the Northern and the Southern Hemispheres (e.g. Blackburn 1950; Reis and Dean 1981; Olney 1983; Arnott and McKinnon 1985). Spawning of anchovies in the most upstream section of the estuary would reduce the chances of egg and larval loss from the system, as the incubation period for their eggs is very short (i.e. two days or less, see Arnott and McKinnon 1985) and the newly hatched larvae are poor swimmers. In the Gippsland Lakes, anchovy eggs were found over a temperature range similar to that of the Hopkins River estuary, but over a broader salinity range

(Arnott and McKinnon 1985). Anchovies appeared to prefer higher water temperature and higher salinity conditions for spawning than was found for the black bream.

The present study showed that the deep pools of Jubilee Park and Tooram Stones are important breeding sites for the black bream and confirms the relationship between black bream spawning and the hydrodynamic cycle of the Hopkins River estuary, as first suggested by Sherwood and Backhouse (1982). Results also indicated that the Jubilee Park deep pool may also be an important breeding area for the estuary perch and the Tooram Stones deep pool for anchovy. The importance of these sites may relate in part to their offering a deep area within which the fish can congregate to spawn. Probably of greater importance, however, are the prevailing moderate salinity and high dissolved oxygen conditions present at this site during salt-wedge emplacement (Newton 1994). Prior to a flood event, conditions would be less favourable for spawning, with sub-halocline waters of the salt-wedge being largely deoxygenated and with salinities in the high twenties (Sherwood and Backhouse 1982; Sherwood 1985; Newton 1994). Although salinities of 11 to 18 have been reported as necessary for the spawning of black bream to occur (Butcher 1945), evidence from the present study suggests that higher salinities of 20 to 25 were required for black bream spawning in the Hopkins River estuary. It is likely that increasing salinity, coupled with decreasing dissolved oxygen concentrations in the deeper waters of the pools from early summer onwards, leads to the diminished spawning activity of the bream. The general reliability of the hydrological cycle and the presence of deep protected spawning sites (i.e. the deep pools) most likely contribute to the Hopkins River estuary being an important and productive spawning area for black bream and possibly other fish species such as anchovy.

Ichthyoplankton in Relation to Zooplankton Cycles

In the Hopkins River estuary, the late-autumn peak in concentration of fish larvae closely followed the early-autumn peaks in abundance of total zooplankton, calanoid nauplii and meroplankton (Newton 1994). These organisms are potential prey of fish larvae (Russell 1976; Hunter 1981; Whitfield 1983; Houde and Alpern Lovdal 1984; Gaughan 1992). The two major sources of mortality for fish larvae are starvation and predation, with the smaller larval stages being the most vulnerable (Hunter 1981). Thus, the timing and location of spawning of adult fishes, and the resultant temporal and spatial distribution of eggs and larvae, would influence the degree to which ichthyoplankton are exposed to these potential sources of mortality.

Gudgeon and goby larvae were in the plankton for extended periods of over five months. This feature, combined with the high densities of zooplankton over

summer, autumn and early winter, suggests that prey densities would not be limiting for these fish larvae. Densities of zooplankton were consistently in the order of 10^5 m^{-3}, and densities of calanoid nauplii were generally above 10^4 m^{-3}. In comparison, mean concentration of fish larvae was generally less than 100 m^{-3}. Threshold prey densities for the survival of fish larvae are difficult to determine in the field and there are few published data. However, laboratory studies are generally regarded as providing overestimates, i.e. 10^5–10^6 m^{-3} (Houde and Schekter 1980; Hunter 1981; Townsend 1983; Houde and Alpern Lovdal 1984). It is unlikely that predation by fish larvae had an impact on the zooplankton community of the Hopkins River estuary, because zooplankton densities were consistently high (apart from during flood periods). It is therefore likely that the threshold prey density was generally exceeded for these estuarine fish larvae, which added to their enhanced survival.

The November peak in concentration of fish larvae, comprised mainly of black bream larvae, was in synchrony with the ascending limb of the zooplankton density curve. This period coincided with the mass hatching of calanoid nauplii from dormant eggs as the copepod populations were re-established after flooding of the estuary and subsequent reformation of the salt-wedge (Newton 1994). It is likely that the early larval period of black bream is short; one disadvantage of such a strategy is that there is an increased probability of mismatch with the optimum prey field. Therefore, the post-flood spawning behaviour of black bream in the Hopkins River estuary would be optimal to coincide with the availability of copepod nauplii, on which the young preflexion larval stages exclusively feed (Willis 1991). In addition, interspecific competition for food would be reduced for black bream larvae during late spring, because the peak in goby/gudgeon spawning occurred after this time. Therefore, the black bream does appear to conform to the strategy of the 'match–mismatch' hypothesis of Cushing (1975, 1990; see also Bollens et al. 1992).

The limited spawning area for black bream, as occurs at the Jubilee Park deep pool, may increase the vulnerability of newly hatched larvae to cohabiting predators. For example, medusae are known to be important predators of fish eggs and larvae, with feeding rates of up to 102 larvae day^{-1} (Arai and Hay 1982; Bailey 1984; Purcell 1992). The main planktonic predator in the Hopkins River estuary is the medusa Australomedusa baylii. However, predatory pressure from this medusa would have a limited affect on black bream larvae, as the latter peak in November, before the post-flood re-establishment of the medusa population in summer (Newton 1994).

In conclusion, the comparatively high zooplankton prey densities available in the Hopkins River estuary are probably adequate for fish larvae, given that the smaller, newly planktotrophic larvae are efficient at capturing prey

(e.g. see Gaughan 1992). Possible seasonal limitations on prey availability could occur if specific fish larvae had a preference (e.g. for nutritional reasons) for certain zooplankters such as the meroplanktonic larvae of decapods, polychaetes and molluscs, which are prevalent mainly over summer and autumn. For example, although copepods and their nauplii were the primary food of the larval fish assemblage in Wilson Inlet, WA, other zooplankton types were also eaten and the larvae of different species adopted different feeding strategies, indicating that resources were partitioned to some degree (Gaughan 1992). In this respect, the summer spawning of gobies may be related in part to the availability of a wider selection of food types for larvae, as a variety of meroplankters are abundant at this time (Newton 1994). In addition, extended spawning times and presence of fish larvae in the plankton would allow larvae to exploit abundant food resources over several months and thereby grow quickly into the juvenile stage (Bollens et al. 1992). Extended larval presence in the plankton, combined with the apparent high density of food available to fish larvae in the Hopkins River estuary, to some extent obviates the 'match–mismatch' hypothesis of Cushing (1975, 1990) and suggests that this hypothesis may be less relevant in the estuarine than in the marine environment.

Acknowledgments

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