

Reproductive biology and early life history of the marine teleost *Platycephalus speculator* Klunzinger (Platycephalidae) in a temperate Australian estuary

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A description is given of the seasonal trends exhibited by gonadosomatic indices, gonadal maturation and oocyte diameters of different age classes of the flathead, *Platycephalus speculator*, in Wilson Inlet, a seasonally closed estuary on the south coast of Western Australia. These data indicate that, although sexual maturity is attained by the vast majority of males at the end of the first year, it is delayed for a further year in females. Breeding occurs predominantly during the summer and early autumn (December to March). The presence of late stage eggs and preflexion larvae between January and March of 1988, when a sand bar was present across the mouth of the inlet channel, demonstrates that this marine species spawns in the estuary. Spawning also occurred within the estuary in the following year, even though the estuary mouth was open during the breeding period. Although *P. speculator* typically spawns at sea, spawning in Wilson Inlet takes place at salinities less than 30‰, i.e. below full strength sea water. The distribution of oocyte diameters and the presence of mature eggs and post-ovulatory follicles in the ovaries of many fish indicate that *P. speculator* spawns more than once in a breeding season. Late stage eggs of *P. speculator* are pelagic, ca 0.8 mm in diameter and possess embryos with an unpigmented yolk sac containing a single, pigmented oil globule. The larvae are pelagic and characterized by a relatively large and wide head bearing a series of spines, a moderately long gut, an elongated and compressed tail, large fan-shaped pectoral fins and 25 or 26 myomeres. Flexion of the notochord occurs between 5 and 7 mm and settlement takes place at approximately 13 mm.

Key words: *Platycephalus speculator*; gonadal development; spawning; estuary; larval development.

I. INTRODUCTION

The majority of fish found in estuaries belong to species that spawn at sea and there are few species which complete their life cycles in estuaries (Haedrich, 1983; Dando, 1984; Claridge *et al.*, 1986; Potter *et al.*, 1990; Tayler, 1990). The occurrence of marine species in estuaries tends to be either irregular and in small numbers or more seasonal and in large numbers. These two groups have been referred to as marine stragglers and marine estuarine-opportunists respectively, the latter consisting mainly of species that utilize estuaries as nursery areas (Lenanton & Potter, 1987).

Estuaries of the southern regions of Australia and Africa typically comprise large central basins connected to the sea by narrow entrance channels (Potter *et al.*, 1986, 1990). Many of these estuaries have been landlocked for variable periods during the recent past, due to the formation of sandbars across the mouths of their entrance channels (Bird, 1984; Hodgkin & Kendrick, 1984; Lenanton & Hodgkin, 1985; Bally, 1987). Today, estuaries such as Wilson Inlet and that of the Bot River on the southern coasts of Western Australia and South Africa respectively, now

close periodically, whereas others are either permanently closed or open (Lenanton & Hodgkin, 1985; Bally, 1987). The landlocking of estuaries in southern Australia could account for a higher than normal prevalence of teleost species that breed in the estuaries of this region (Potter *et al.*, 1986, 1990).

The period in each year during which the sand bar remains breached in Wilson Inlet is highly variable and, in years when winter rainfall is low, the bar can form as early as December, i.e. in the early summer (Hodgkin & Clark, 1988). Since many marine species of teleost spawn in the summer in Western Australia (Thompson, 1957), the closure of the estuary at this time would prevent both the emigration to marine spawning areas of any marine estuarine-opportunists that have remained in the estuary and an immigration of larvae and/or juveniles from marine waters. One such species that could be affected is the flathead *Platycephalus speculator* Klunzinger, which is distributed along the southern coast of Australia and is abundant in the estuaries and coastal waters of southern Western Australia (Hutchins & Swainston, 1986; Lenanton & Potter, 1987). In Wilson Inlet, this benthic predator can live for up to 12 years of age and reach approximately 70 cm in length (Hyndes *et al.*, 1992). Information on whether *P. speculator* can breed in estuaries, as well as in marine waters, is important since this species contributes to the recreational and commercial fishery of the southern coast of Western Australia (Lenanton, 1984). Despite the fact that the Platycephalidae contains 60 species and is distributed throughout the Indo-Pacific region (Paxton & Hanley, 1989), there are only limited data on the reproductive biology of any species in this family (e.g. Colefax, 1938; Fairbridge, 1951). Furthermore, the only descriptions of the larvae of identified species of this family are those given for *Platycephalus indicus* (Linnaeus) and *Onigocia spinosa* (Temminck and Schlegel) collected from marine waters off Japan and for *Kumococcius detrusus* (Jordan and Seale) from China (Fujita & Ueno, 1956; Chang *et al.*, 1980; Zhang *et al.*, 1985; Kojima, 1988).

The present study describes the pattern of gonadal, oocyte and larval development of *Platycephalus speculator* in Wilson Inlet. These data are then used to determine the breeding period and to demonstrate that *P. speculator* can spawn within seasonally closed estuaries such as Wilson Inlet.

II. MATERIALS AND METHODS

SAMPLING LOCALITY AND REGIME

Wilson Inlet is located on the southern coast of south-western Australia at 34°50' S and 117°25' E. The 48 km² estuary basin of this system is generally less than 2 m in depth and is fed by two major tributary rivers. The estuary opens seasonally to the Southern Ocean by a narrow 1 km long, shallow entrance channel (Hodgkin & Clark, 1988).

Juvenile and adult *Platycephalus speculator* were collected within Wilson Inlet using beach seines during the day and gillnets and otter trawls at night. The beach seine, which consisted of 21 m long wings (stretched mesh = 51 mm) and a 3 m pocket (stretched mesh = 9.5 mm), fished to a depth of 1.5 m. Each of the two sunken composite gillnets were 180 m long and comprised six 30 m long panels with sequential stretched mesh sizes ranging from 38 to 102 mm. Gillnets were set prior to dusk and collected shortly after dawn. The otter trawl net, which was 5 m long and had a 2.6 m wide and 0.5 m deep mouth, consisted of 51 mm stretched mesh in the wings and 25 mm in the pocket.

Samples were collected bimonthly at sites throughout Wilson Inlet between September 1987 and April 1989. Further samples were obtained by gillnetting at a site in the lower estuary during the intervening months. Juvenile *P. speculator* were also obtained from

samples taken by a 21.5 m long beach seine (9 and 6 mm stretched mesh in the wings and pocket, respectively) throughout the estuary in each month between January and April 1988.

Two conical plankton nets were used to collect larvae at six sites spaced throughout Wilson Inlet. Each net, comprising 0.5 mm mesh, was 2 m long and had a mouth diameter of 0.6 m. Both nets were towed at night below the water surface at each site for 10 min at a boat speed of 1.0 to 1.5 m s⁻¹.

The bottom salinity and bottom temperature of the water were recorded at each site at the time of sampling. Data on daylength in the middle of each month in the region of Wilson Inlet were obtained from the Perth Observatory charts. Data on the opening and closing dates of the sand bar at the entrance of this estuary prior to 1989 were obtained from Lukatelich *et al.* (1984) and the Western Australian Water Authority.

LABORATORY PROCEDURES

The total length and weight of each fish were measured to the nearest 1 mm and 0.1 g, respectively. Gonads were removed, weighed to the nearest 0.01 g and staged (I–VII) according to the criteria of Laevastu (1965). Gonadal stages are as follows: I, virgin; II, maturing virgin; III, developing; IV, maturing; V, mature; VI, spawning; VII, spent. Gonadosomatic indices (GSI) were determined from the equation $W1/W2 \times 100$, where $W1$ = wet weight of gonad and $W2$ = total wet weight of fish. Ovaries of a random subsample of 10 fish from each month were placed in Bouin's fixative for 24 h, dehydrated in ethanol and embedded in paraffin wax. Transverse sections (6 μ m) of the mid-region of each ovary were stained in Mallory's trichome. The longest and shortest diameters of 30 oocytes from the centre of each section were recorded to the nearest 1 μ m. The mean of these two measurements is subsequently referred to as the diameter of each oocyte. The mean diameters of 100 loose hyaline oocytes, which had become detached from spawning (stage VI) ovaries when these ovaries were being removed from the body cavity, were also recorded. The terminology for the oocyte stages follows that given in Khoo (1979). The translucent zones in the otoliths of *P. speculator*, which have been shown to be formed annually (Hyndes *et al.*, 1992), were counted in all fish used for gonadal studies.

Plankton samples collected between December 1987 and February 1988 from four of the six sampling sites contained a number of pelagic, late stage eggs that were morphologically very similar to the pelagic eggs of *P. indicus* (Fujita & Ueno, 1956; Chang *et al.*, 1980). Since *P. speculator* was the only platycephalid recorded in extensive beach and gillnet samples collected throughout Wilson Inlet between 1987 and 1990, it was assumed that these eggs belonged to this species. This conclusion is consistent with the fact that, unlike those of other species known to spawn within this estuary, these eggs are pelagic (F. J. Neira & I. C. Potter, in prep.). Further rationale for the identification of these eggs as those of *P. speculator* is given in the Results. The diameters of these eggs were measured to the nearest 0.01 mm.

The body length (B.L.) of each *P. speculator* larva, i.e. notochord length in preflexion and flexion larvae and standard length in postflexion larvae, was measured to the nearest 0.1 mm using a stereomicroscope fitted with an eyepiece micrometer.

Eighteen *P. speculator* larvae, ranging in B.L. from 1.6 to 12.8 mm, were used to describe the change in morphology, pigmentation, meristics and morphometrics during development. A further nine newly-settled juveniles, ranging in body length from 15.5 to 25.5 mm, were also examined. All body intervals, which were each measured to the nearest 0.1 mm, have been expressed as a percentage of body length. The designation of the different larval stages, the general terminology and the body intervals measured, each follow those given in Leis & Trnski (1989), whereas the meristic counts and the terminology used to describe the head spination follow those described by Neira (1989).

III. RESULTS

TIME OF BAR CLOSURE AND ENVIRONMENTAL VARIABLES

Each year, the sand bar at the mouth of Wilson Inlet is breached artificially when the water height within the system reaches a certain level (Hodgkin & Clark, 1988).

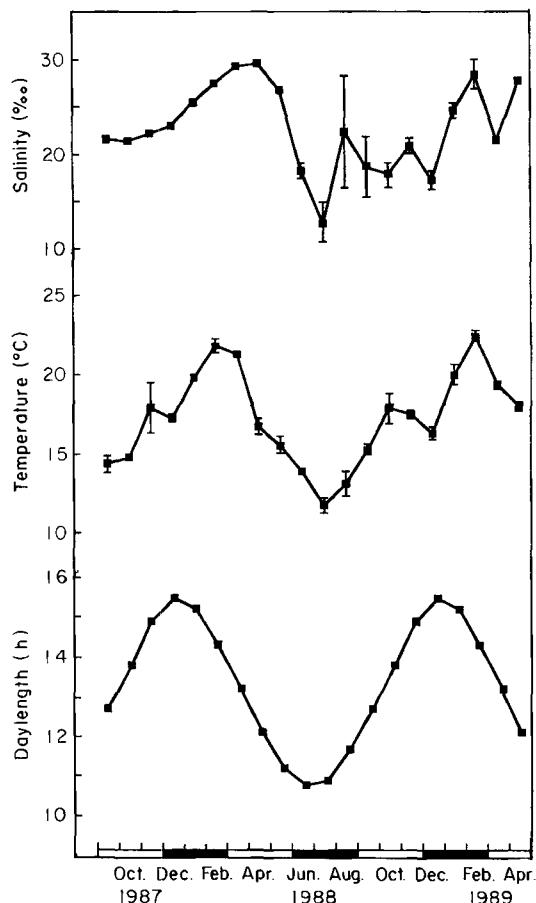


Fig. 1. Mean monthly salinities and water temperatures \pm 1 s.e. recorded at the six sampling sites in Wilson Inlet. Daylengths in the middle of each month in the Wilson Inlet region were obtained from Perth Observatory charts. The black and white boxes on the horizontal axis represents the summer and winter seasons and the spring and autumn seasons, respectively.

The entrance channel of this estuary remained open for 67 days between mid-October and late December 1987 and for 334 days between mid-June 1988 and mid-May 1989. The mean period in which the channel has been open annually in the 34 years prior to 1989 is 181 days (Lukatelich *et al.*, 1984; Western Australian Water Authority).

Since both bottom salinity and bottom water temperature varied little between sites on each sampling occasion, the values for these variables in each month have been pooled to provide an overall mean (Fig. 1). Mean bottom salinity increased from about 22‰ in September and October of 1987 to a peak of 29.8‰ in April 1988, before declining to a minimum of 12.8‰ in July 1988 (Fig. 1). Mean salinity subsequently rose to 28.5‰ in February 1989. Mean bottom water temperatures showed similar seasonal trends to those of the mean bottom salinities (Fig. 1). Mean temperatures reached a maximum of about 22°C in February in both 1988 and 1989 (Fig. 1). The minimum mean temperature of 12.0°C was recorded in July

1988. Daylength reached a maximum of 15.5 h in December and fell to a minimum of 10.8 h in June (Fig. 1).

GONADAL DEVELOPMENT

Preliminary examination of the data showed that the seasonal trends in gonadal development and GSIs of those male and female *P. speculator* whose otoliths possessed a single translucent zone, differed from those of the corresponding sex of fish possessing two or more such zones. However, no difference could be detected between these reproductive variables in groups of either males or females in which there were either two, three or four translucent zones. For this reason, the monthly gonadal data for fish with otoliths possessing two or more translucent zones have been pooled and considered separately from those of fish in which the otoliths possessed only one translucent zone.

Since larvae and the smallest juveniles first appeared in December to March (Hyndes *et al.*, 1992), spawning was assumed to occur within this period. Thus, because the initial translucent zone first becomes apparent in the otoliths of the corresponding cohort of fish in the following October, its appearance occurred shortly before the fish were 1 year old. However, it was considered convenient to refer to those fish which possessed one translucent zone in their otoliths in October and November, as well as in subsequent months, as constituting the 1+ age class. Such an approach, which was similarly adopted for fish possessing otoliths with two or more translucent zones, enables the trends shown by the same cohort to be followed through from prespawning to postspawning.

The gonads of female fish caught between November and February, at the end of their first year of life, were mainly at stages II and III (74%) and none of the remaining 26% of the gonads of these fish, which belonged to the larger members of this group, had progressed beyond stage V (Fig. 2). In contrast, most of the gonads of $\geq 2+$ females at the same time of the year were at stages V (mature), VI (spawning) or VII (spent) (Fig. 2). It is therefore assumed that most, if not all, females spawn for the first time when they are approximately 2 years old. Approximately 90% of the testes of 1+ males, and all of those of $\geq 2+$ males, exceeded stage III between November and April. However, while stage VI (spawning) testes were not found until February in 1+ fish, they were present as early as December in $\geq 2+$ males. It is thus concluded that, while spawning occurs in the vast majority of males at the end of their first year of life, it is delayed until late in the breeding season.

The mean monthly GSIs of 1+ females showed no conspicuous seasonal trends and never exceeded 1.5 (Fig. 3). The mean monthly GSIs of $\geq 2+$ females rose from 1.3 in September 1987 to a well defined peak of 5.8 in December, before declining to 1.1 in April (Fig. 3). Mean GSIs subsequently remained low (*ca* 1%) until October 1988, after which they increased to approximately 4.5 between November 1988 and March 1989, before declining precipitously to 1.5 in April (Fig. 3). The seasonal trends exhibited by the mean monthly GSIs of $\geq 2+$ males paralleled those just described for $\geq 2+$ females, with mean GSIs reaching their maxima (3.5–3.8) in the summer of both 1987/1988 and 1988/1989 (Fig. 3). Although the mean GSIs of the 1+ males also showed similar seasonal trends, the maximum mean monthly values were considerably less than that of $\geq 2+$ males (Fig. 3).

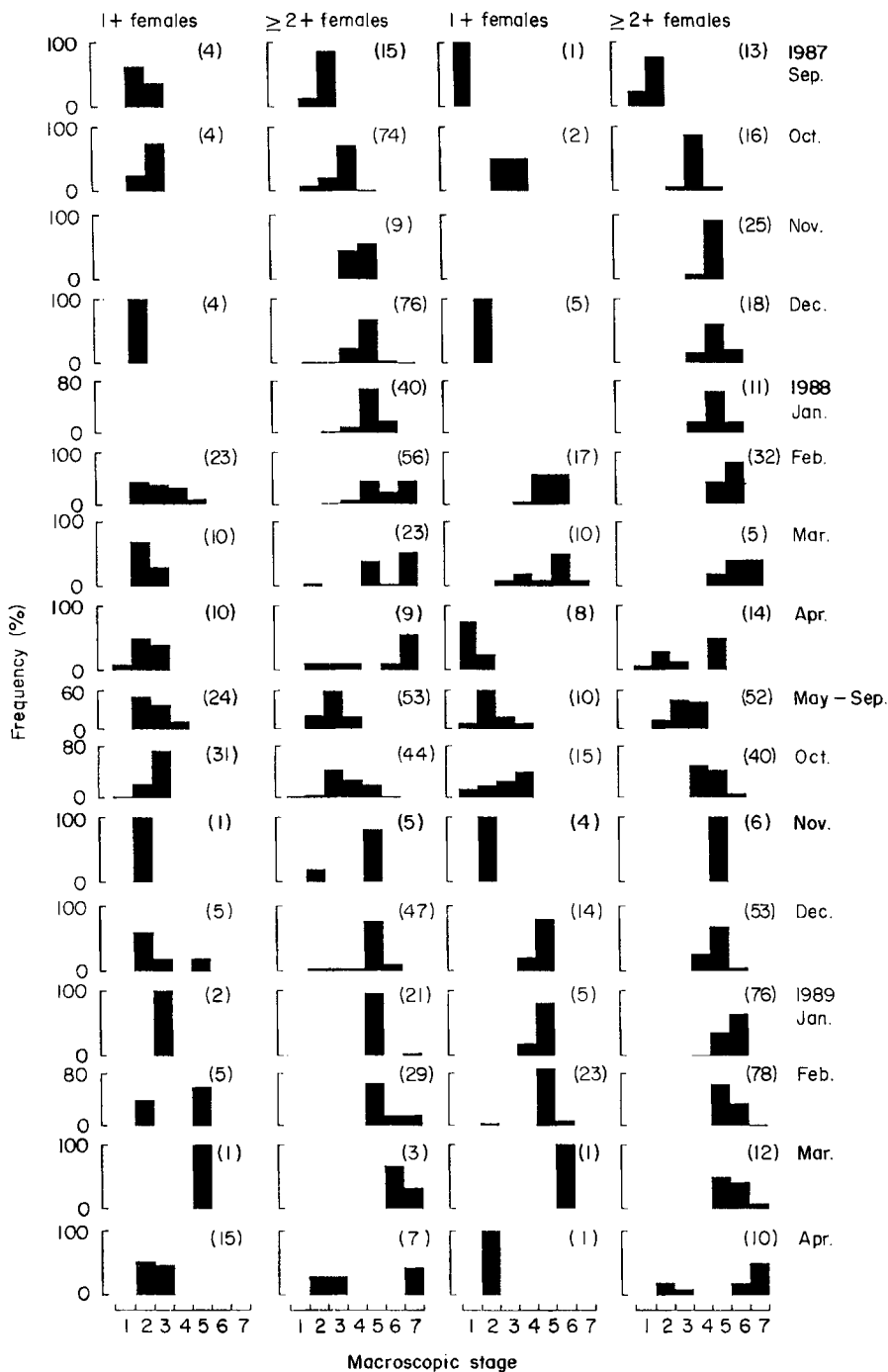


FIG. 2. Frequency of occurrence of sequential stages in the development of the gonads of 1+ and $\geq 2+$ females and males of *Platycephalus speculator* caught in Wilson Inlet between September 1987 and April 1989. Gonad stages follow the criteria of Laevastu (1965). Note that in this and Figs 3 and 4, the 1+ and $\geq 2+$ refer to the number of translucent zones. Since these zones are formed in October/November, just before the birthday of 1 January, they also include results for fish which were approaching 1 and 2 years of age respectively.

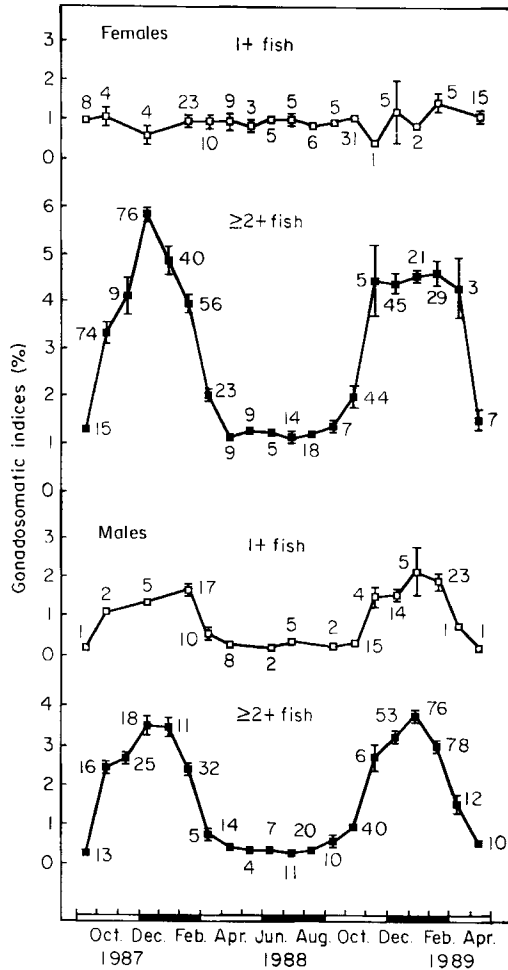


FIG. 3. Mean gonadosomatic indices \pm 1 s.e. for 1+ and $\geq 2+$ females and males of *Platycephalus speculator* caught in Wilson Inlet between September 1987 and April 1989. The black and white boxes on the horizontal axis represent the summer and winter seasons and the spring and autumn seasons, respectively.

In all months, the group of smallest oocytes in $\geq 2+$ fish produced a well defined mode at about $30 \mu\text{m}$ (Fig. 4). These oocytes were at the early perinuclear stage. The upper end of the range of oocyte diameters increased from $120 \mu\text{m}$ in August to between 550 and $630 \mu\text{m}$ in October to December, when secondary growth phase oocytes, including yolk granule oocytes, were present. The diameters in these and subsequent months formed a continuum throughout the full range of oocyte sizes. Since fully-hydrated oocytes collapsed on sectioning, as is frequently the case with those of teleosts (Macer, 1974; Treasurer & Holliday, 1981; Chubb & Potter, 1984), it was not possible to obtain a measurement of the diameters of intact mature eggs in sectioned material. The large, hydrated eggs, which had become detached during the removal of the ovary from the body cavity in December, January and February and stored in 70% alcohol, ranged in diameter from 530 to $850 \mu\text{m}$ (Fig. 4). The maximum diameter of oocytes in sectioned material declined from

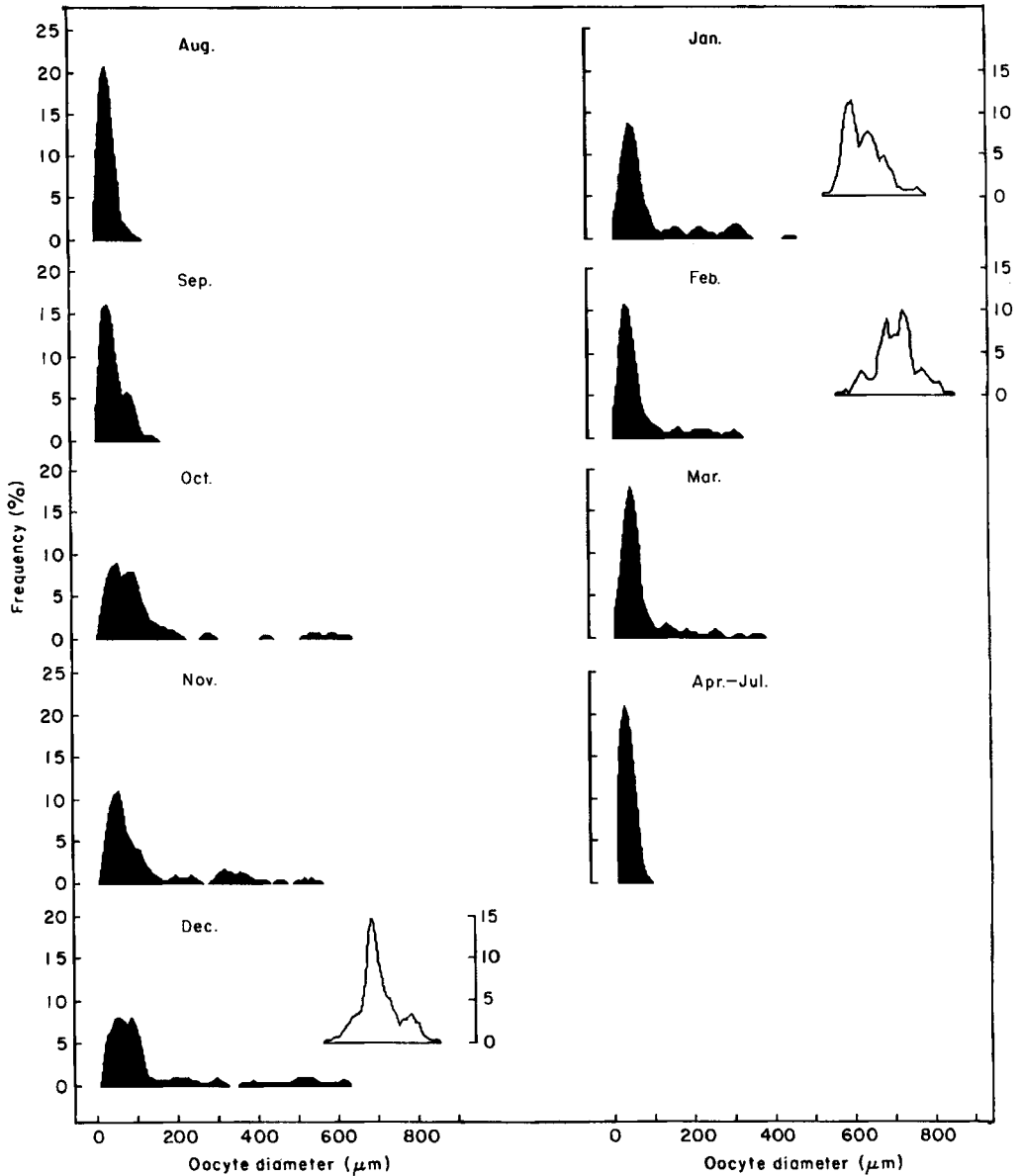


FIG. 4. Frequency distributions for oocyte diameters from the ovaries of $\geq 2+$ *Platycephalus speculator* caught in Wilson Inlet, using data collected between August 1987 and April–July 1989. Shaded area refers to data on oocytes in sectioned material, whereas the unshaded areas refer to loose hydrated oocytes. Data have been smoothed using a moving average of three.

300–450 μm between January and March to less than 100 μm between April and July, the latter value being similar to the maximum diameter recorded in the previous August.

The oocytes from individual stage V and VI ovaries between October and March also formed a size continuum throughout the full range of oocyte sizes. This reflects the fact that both primary and secondary growth phase oocytes at different

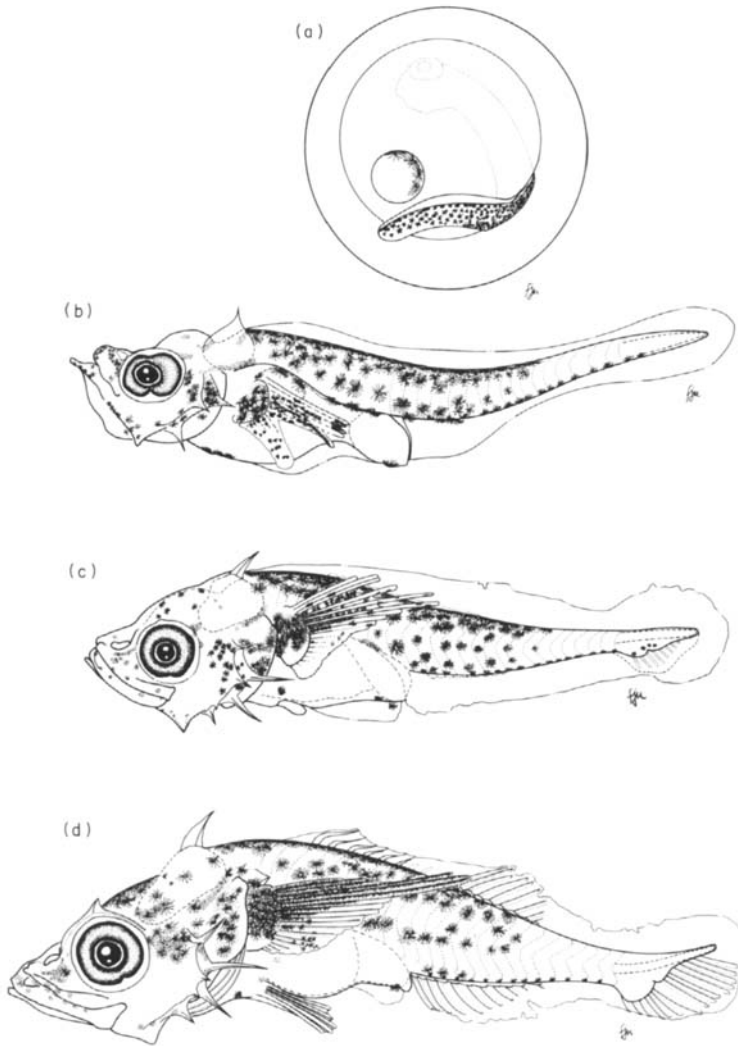


FIG. 5. Late stage egg (a = 0.79 mm diameter) and preflexion (b = 2.74 mm, c = 4.63 mm) and flexion (d = 5.52 mm) larvae of *Platycephalus speculator*, illustrated from material collected in Wilson Inlet. Egg and larva illustrated in (d) were obtained in February 1988, whereas the larvae illustrated in (b) and (c) were collected in March 1989.

stages of development were present in all of these ovaries. Furthermore, the presence of collapsed hyaline oocytes and post-ovulatory follicles in many stage VI ovaries demonstrated that some eggs had already been discharged.

EGG AND DEVELOPMENT OF LARVAE

Eggs

Late stage eggs of *P. speculator* (0.77–0.83 mm diameter) are pelagic, spherical and transparent, i.e. they possess a smooth chorion [Fig. 5(a)]. The yolk sac (0.59–0.69 mm diameter) is unsegmented and has no pigment. A single, pigmented oil globule (0.14–0.19 mm diameter) is located towards the posterior portion of the

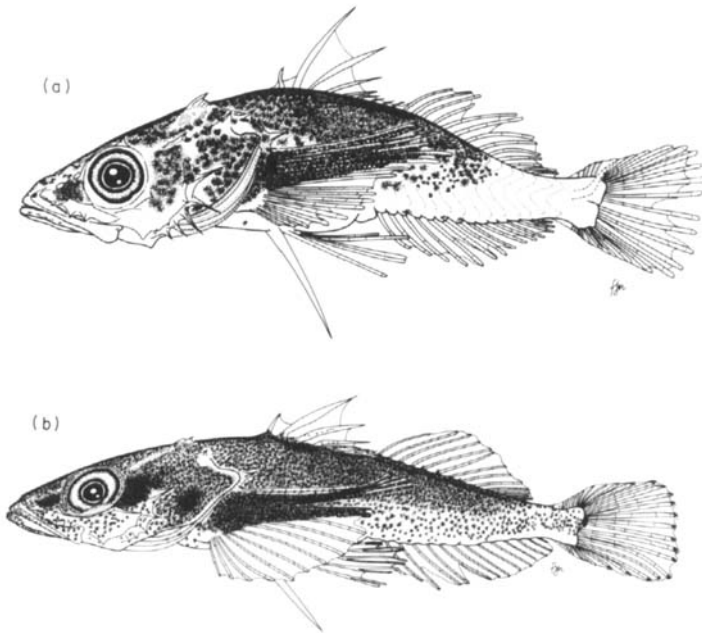


FIG. 6. Postflexion larvae (a = 9.30 mm, b = 12.30 mm) of *Platycephalus speculator*, illustrated from material collected in Wilson Inlet in April 1989.

yolk sac. Melanophores are scattered over the whole body surface of embryos except the eye primordia [Fig. 5(a)]. The diameter of these late stage eggs falls within the range of the diameters of mature eggs found in the body cavity of females of this species (Fig. 4).

While the diameter of these eggs and their possession of a single pigmented oil globule is the same as in *P. indicus*, the yolk sac of the late stage embryos of *P. indicus* possesses pigment (Fujita & Ueno, 1956; Chang *et al.*, 1980; Ikeda & Mito, 1988).

Identification of larvae

Larvae were identified as belonging to the Platycephalidae through a combination of characters including head spination, the large, fan-shaped pectoral fins and a number of myomeres that lies within the 25–28 characteristic of this family (Leis & Rennis, 1983). Postflexion larvae were identified as those of *P. speculator* by dorsal and anal fin ray counts of VIII–IX + 13–14 and 14 respectively (Last *et al.*, 1983). Preflexion and postflexion larvae were arranged in a series, according to the degree to which the pectoral fins had developed, and the way in which the body pigmentation and head spination changes.

Description of larvae

Larvae of *P. speculator* are pelagic and characterized by a relatively large and wide head bearing a series of spines, a moderately long gut, an elongate and compressed tail, fan-shaped pectoral fins and either 25 or 26 myomeres (Figs 5 and 6). The head is initially small and moderately compressed, but becomes elongated

TABLE I. Range in body lengths and body intervals recorded for larval and newly-settled *Platycephalus speculator* in Wilson Inlet. Body intervals are expressed as a percentage of body length

Stage	<i>n</i>	Body length (mm)	Head length	Preanal length	Pectoral fin length	Body depth at pectoral fin base
Preflexion	9	1.6-4.6	19.0-29.7	48.4-53.6	11.7-26.4	11.7-26.4
Flexion	3	5.1-5.5	28.6-36.8	53.2-57.4	27.5-35.3	21.4-22.2
Postflexion	6	7.9-12.8	34.8-41.3	58.9-62.5	29.8-34.8	18.3-26.6
Settlement	9	15.5-25.5	34.8-40.7	55.8-62.2	22.2-25.9	12.7-17.7

and depressed as the snout lengthens and flattens during growth. The relative length of the head increases from approximately 20% B.L. in preflexion larvae to about 40% B.L. in postflexion larvae (Table I). The eyes are round and laterally positioned in all larval stages, but become slightly ovoid and migrate to a dorsal position after settlement. A small gas bladder is visible above the anterior portion of the gut only in preflexion larvae. The gut is moderately long and extends to the mid-body region in preflexion larvae [Fig. 5(b,c)] and approaches 60% B.L. in newly-settled specimens. There is no gap between the anus and the fully-formed anal fin. Notochord flexion occurs between body lengths of 5 and 7 mm and individuals settle at approximately 13 mm [Table I, Fig. 5(b)]. Scales were observed in settled fish over 30 mm.

Fin development

The incipient rays of the pectoral fins were present in the smallest larva examined (1.6 mm) and all 18-19 rays are formed soon after flexion is completed. Pelvic buds are visible by 4.5 mm and all 1,5 rays are formed by 5.5 mm [Fig. 5(c,d)]. The single spine of each pelvic fin becomes very elongate in postflexion larvae (Fig. 6). Elements of the dorsal and anal fins appear simultaneously at about 4.5 mm and all are completely formed by 8.0 mm. The rays of the caudal fin appear by 4.5 mm and all have developed by 7.5 mm.

Pigmentation

Pigment is scattered on the head, dorsal surface of the gut, pectoral fins and trunk of all larval stages [Fig. 5(b-d)]. While pigment is particularly intense on the anterior dorsal surface of the trunk, the dorsal and lateral surfaces of the tail remain unpigmented throughout development. Pigment on the head, trunk and tail increases during development until it covers most of these areas in postflexion larvae [Fig. 6(b)]. Melanophores on the lateral and ventral surfaces of the gut and of the ventral surface of the trunk and tail, start to disappear before settlement. After settlement, the whole ventral surface (i.e. from the tip of the lower jaw to the base of the caudal fin) loses its pigmentation. Pigment on the pectoral fin is concentrated on the base of this fin and along the upper six or seven rays (except the first), whereas the lower nine or 10 rays remain unpigmented. The other fins remain unpigmented, except for a few melanophores on the third, fourth and fifth spines of the dorsal fin [Fig. 6(b)].

Head spination

One anterior and two posterior preopercular spines and a parietal spine are present on the smallest preflexion larva illustrated [Fig. 5(b)]. The number of anterior preopercular spines increases to three by 4 mm and the number of posterior preopercular spines increases to five by approximately 8 mm. The anterior and posterior preopercular spines merge before settlement [Fig. 6(b)]. The first and second of the posterior preopercular spines become the longest after flexion [Fig. 6(a)] and remain after settlement. The parietal spine also remains after settlement but becomes blunt. A supraocular spine appears at about 4.5 mm and remains very small after settlement. Three to seven small infraorbital spines appear in postflexion larvae between 9.3 and 12.8 mm, of which the two anterior-most spines remain after settlement. Cleithral, supracleithral, post-temporal and sphenotic spines form at the time of notochord flexion and all, except the sphenotic, remain in newly-settled fish.

The development of the larvae of *P. speculator* follows a similar pattern to that of *P. indicus*. Thus, the body length at which *P. speculator* hatches (> 1.6 mm), undergoes notochord flexion (5.0–7.0 mm) and reaches the settlement stage (> 13.0 mm), each fall within the ranges recorded for these events in *P. indicus* (Fujita & Ueno, 1956; Chang *et al.*, 1980). However, the dorsal and anal fins form at smaller body lengths in *P. speculator* than in *P. indicus* (4.5 v. 5.9 mm, respectively) (Chang *et al.*, 1980).

COLLECTIONS OF EGGS AND LARVAE

A total of 102 late stage eggs and 10 larvae of *P. speculator* were collected in Wilson Inlet during the period when the estuary had been closed for between 25 and 91 days (January–March 1988). Of the eggs, 98% were collected in January. The lengths of the larvae, which were caught at sites throughout the estuary, ranged from 1.6 mm (preflexion larvae) to 12.8 mm (postflexion larvae). The lengths of the 28 larvae caught between December 1988 and April 1989, when the estuary was open to the sea, ranged from 1.7 to 12.1 mm.

IV. DISCUSSION

The data reported in this paper demonstrate that, within Wilson Inlet, the females of *P. speculator* rarely, if ever, reach sexual maturity until they are 2 years old. In contrast, the vast majority of the males reach maturity at the end of their first year of life, even though this is not attained as early in the spawning season as is the case with older males. Our results also provide strong circumstantial evidence that the population of *P. speculator* in Wilson Inlet typically spawns between December and April. This conclusion is based mainly on the fact that, in both years of our study, a combination of both spawning (stage VI) and spent (stage VII) ovaries and testes were only found in these months. Such a conclusion is also consistent with the presence of fully-hydrated eggs in the ovaries used for histological sections from December to February (Fig. 4). Although hydrated eggs were not found in any of the sectioned ovaries in March, large mature oocytes were still present in a few fish in this month. However, the observation that no ovaries exceeded stage V in April 1988, and only a few were at stage VI in April 1989

strongly suggests that spawning activity is limited after March. This view is supported by the observation that, in those ovaries used for histological sectioning, the majority of oocytes in April were in the primary growth phase and had a maximum diameter of only 110 μm . The trends shown by the GSIs of $\geq 2+$ males and females are also consistent with the conclusion that spawning occurs between December and April. The above data very strongly indicate that spawning peaks at some time between December and February and it was for this reason that the nominal birthday of 1 January was given for the population of *P. speculator* in Wilson Inlet (Hyndes *et al.*, 1992).

The presence of fully mature and spawning gonads in female *P. speculator* in Wilson Inlet during a period when this estuary was isolated from the sea, suggests that this species spawns within this system. However, it should be recognized that, in the case of species such as the sea mullet (*Mugil cephalus* Linnaeus) and yellow-eye mullet [*Aldrichetta forsteri* (Valenciennes)], the presence of fully mature and spent ovaries in individuals caught in estuaries does not mean that spawning necessarily occurs within these systems. In these latter two species, the prevention of migration to their marine spawning areas results in the resorption of eggs and thus a failure to spawn (Wallace, 1975; Chubb *et al.*, 1981). The absence of the larvae of species such as *Pomatomus saltatrix* (Linnaeus), *Argyrosomus hololepidotus* (Lacépède) and *Rhabdosargus sarba* (Forsskal) in extensive sampling of the estuaries of south-western Australia where their adults are often numerous, also provides no evidence that those other relatively long-lived species spawn within these systems. However, irrefutable evidence that *P. speculator* is capable of spawning successfully within Wilson Inlet comes from the collection of eggs and all larval stages of this species in the estuary between January and March 1988, when the presence of a bar across the estuary mouth would have prevented the entry of such early life cycle stages from the sea. It is also worth noting that, even though the bar did not form until April in 1989, no *P. speculator* larvae were found in the large catches of fish larvae taken on flood tides in the entrance channel in either December 1988 or January 1989 (Neira & Potter, 1992). Thus, the presence of eggs and larvae of *P. speculator* within the estuary at this time provides very strong circumstantial evidence that spawning occurs within the estuary even when it is open to the sea. The collection of a comprehensive sequence from the late stage eggs through to late postflexion larvae and early juveniles also indicate that spawning leads to the successful recruitment of a new generation.

Several other platycephalid species are found in estuaries as well as in inshore marine waters of the Indo-Pacific region (Paxton & Hanley, 1989). Since *Platycephalus endrachtensis* Quoy and Gaimard is only found in estuaries in the southern part of its range in Western Australia, it must presumably be capable of spawning in these systems (Potter *et al.*, 1990). However, the data reported in this paper provide the first direct and conclusive evidence of estuarine spawning in a species of flathead.

P. speculator can reach 12 years of age (Hyndes *et al.*, 1992). This is a much longer life span than that of most other species that spawn in the estuarine waters of south-western Australia. The most abundant of these other species belong to families such as the Gobiidae, Atherinidae and Apogonidae, many of which have only 1 or 2 year life cycles (Prince & Potter, 1983; Chrystal *et al.*, 1985; Potter *et al.*,

1986). The tendency for estuaries throughout south-western Australia to become landlocked would have placed specially strong selection pressures on these short-lived species to become adapted to spawning within estuaries (Potter *et al.*, 1986). The ability of *P. specularator* to spawn within Wilson Inlet indicates that the particularly frequent and sometimes protracted periods of closure of those estuaries along the south coast of Western Australia has even had such an influence on a long-lived species such as *P. specularator*. Moreover, the data in the present paper provide strong evidence that *P. specularator* is a multiple spawner, a characteristic that would increase the chances of egg and larval development occurring at some stage under environmental conditions similar to those of the marine environments at the time of breeding.

Although spawning was initiated after daylength, temperature and salinity had each shown a progressive rise, it is worth noting that the GSIs of $\geq 2+$ females remained high (> 4.5) for a far longer period in the summer of 1988–1989 when salinities took longer to reach higher levels ($> 22\text{‰}$) (cf. Figs 1, 3). Despite this implication that, to some extent, spawning may be delayed until salinities become elevated, the main part of the spawning season (December to March) occurred when salinities were always less than 30‰.

The eggs of the majority of species which spawn in estuaries are either benthic or receive some form of parental care. These features help prevent the eggs from being flushed out into the marine environment (Dando, 1984; Whitfield, 1990). Although the eggs of *P. specularator* are pelagic, they would be prevented from being swept out to sea when the entrance channel is closed. Furthermore, the very restricted freshwater discharge and small tidal action within the estuary, during the period when *P. specularator* breeds, would make it unlikely that they would be susceptible to such flushing, even when the entrance channel is open. This view is consistent with the absence of *P. specularator* eggs in numerous plankton samples taken in the inlet channel when it was open to the sea in December 1988 and January 1989.

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