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Reproductive biology and larval development of the terapontid *Amniataba caudavittata*, including comparisons with the reproductive strategies of other estuarine teleosts in temperate Western Australia

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Samples collected monthly from the Swan Estuary between March 1978 and May 1979, together with environmental data for 1977 to 1980, have been used to elucidate various aspects of the reproductive biology of *Amniataba caudavittata* in this estuary. The gonads of *A. caudavittata* started to develop rapidly in the spring, when day length, water temperatures and salinities were increasing markedly. Spawning, which occurred mainly towards the top end of the upper estuary, was initiated in November, when water temperatures and salinities in that region were *c*. 24° C and 9‰, and it peaked in December/January when they were *c*. 27° C and 17‰. Maturity is attained by at least the majority of fish at the end of the second and each subsequent year of life. Although some of the larger 1-year-old fish attained maturity, this occurred in only one of the two tributary rivers, possibly reflecting differences in the salinity regimes in these rivers. Fecundities ranged from 50 000 in a 150-mm fish to 705 000 in a 254-mm fish, with a mean of 310 000. The mature, unfertilized eggs are small and spherical and have a diameter of 560 μm. The larvae are pelagic and characterized by an elongate body, which becomes moderately deep and laterally compressed during development, a short to moderate, tightly-coiled gut, a distinct gap between the anus and the origin of the anal fin and 25 or 26 myomeres. The development of fins and settlement of *A. caudavittata* larvae occurs at a smaller size than in the larvae of other terapontid species previously described. The success of *A. caudavittata* in the Swan Estuary can be attributed in part to its production of very large numbers of eggs at a time when, due to low fresh water discharge and a small tidal range, conditions in the estuary are relatively stable. Comparisons between the biology of *A. caudavittata* and that of other abundant teleosts that spawn in south-western Australian estuaries show that these species exhibit a wide range of reproductive strategies.

Key words: *Amniataba caudavittata*; Terapontidae; gonadal development; spawning; estuaries; larval development; temperate Australia.

I. INTRODUCTION

The Terapontidae is a perciform family, found in the fresh, brackish and marine waters of the Indo-West Pacific (Vari, 1978). The family contains 15 genera and 46 species, of which 30 have been recorded in Australia (Allen & Cross, 1989). One of these species, the yellowtail trumpeter *Amniataba caudavittata* (Richardson), occurs northwards of latitude 33°16′S on the west coast of Australia and in the Northern Territory, Queensland, the Torres Strait and the southern half of New Guinea (Vari, 1978). Although *A. caudavittata* has been recorded in fresh, estuarine, marine and markedly hypersaline waters (Lenanton, 1977; Vari, 1978), it is almost exclusively confined to estuaries in south-western Australia (Potter *et al.*, 1990).

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The relatively few detailed studies of the reproductive biology of terapontids have dealt with freshwater species (Mane, 1934; Lake, 1967*a,b*; Llewellyn, 1973; Beumer, 1979) in all but the case of the marine species *Terapon jarbua* (Forskål) (Miu *et al.*, 1990). Data on the larval development of terapontids are also sparse and there are no descriptions of the larvae of either of the species of *Amniataba* (Leis & Trnski, 1989). There is no information on the environmental conditions that influence gonadal development and the initiation of spawning in *A. caudavittata* or on the region of the estuary in which this species spawns. Moreover, our preliminary results on the fecundity and age at maturity of *A. caudavittata* were clearly inconsistent with those tabulated by Thomson (1957) for this species.

The first aim of the present study was to describe the trends shown by the development of the gonads and oocytes of *A. caudavittata* in the Swan Estuary. These data were then related to the location where the larvae, 0+ recruits and mature fish were caught, in an attempt to elucidate the environmental factors that would be likely to influence gonadal development and the attainment of maturity, and to determine where this species spawns within the estuary. Emphasis was also placed on ascertaining the extent to which maturity is related to the size and age of the fish. The relationship between the fecundity of *A. caudavittata* and body size has been determined and a quantitative morphological description is given of the development of the larvae of this species. Finally, the results were compared with those obtained for other abundant estuarine fish species in temperate Western Australia to help elucidate the basis for the success of these species in the estuaries of this region.

II. MATERIALS AND METHODS

SAMPLING SITES, METHODS AND REGIME

The Swan Estuary comprises a 7·5 km long narrow entrance, two large central basins and the saline regions of the two rivers which discharge into those basins (Loneragan *et al.*, 1989). The Entrance Channel and basins constitute the lower and middle estuary, respectively, whereas the saline reaches of the Swan-Avon and Canning rivers, which discharge into the middle estuary, are regarded as the upper estuary (Chalmer *et al.*, 1976). Sampling for juvenile and adult *Amniataba caudavittata* was carried out between March 1978 and May 1979, using seine nets at 11 sites in shallow waters, gillnets at eight sites in more offshore waters and otter trawls at six sites in deeper water [see Loneragan *et al.* (1989) for location of sampling sites]. Samples were obtained from several or all of these sites at least once monthly with seine nets and otter trawls and bimonthly with gillnets [see Chubb *et al.* (1981) and Loneragan *et al.* (1989) for details of the frequency with which the sites were sampled using the three different methods].

The seine net was 133 m in length and comprised 25·4-mm mesh in the wings and 9·5-mm mesh in the pocket. The composite gillnets, comprising one sunken and one floating net, consisted of ten 20-m long panels, ranging in mesh size from 38 to 102 mm in approximately 7-mm increments. The otter trawl was 5 m long, consisted of 51- and 25-mm mesh in the wings and pocket, respectively, and was towed for 5 min at 3–4 km h^{-1} at each site on each sampling occasion. Seine netting and otter trawling were carried out during the day, while gillnetting was undertaken in the 3 h after sunset.

Day lengths in the region of the Swan Estuary at the time of sampling in each month were obtained from Perth Observatory charts. The surface salinity and water temperature were recorded prior to collecting each sample. The salinities and temperatures at Sites 5, 6 and 9 have been selected as examples of the way these variables change monthly (see

Fig. 1), because the first two sites consistently yielded good catches of fish and the third site provided contrasting data on the GSIs of 1-year-old fish. Sites 5 and 6 are located in the Swan-Avon River at distances of 29 and 38 km from the estuary mouth respectively, while Site 9 is in the Canning River, at a point 22 km from the estuary mouth.

Since the lengths of the 0+ recruits of *A. caudavittata*, at the time they first appeared in samples, were very similar in each year between 1977 and 1980 (Wise *et al.*, in press) spawning must have occurred in the same period in each of those years. For this reason, the trends shown by the above environmental variables, which might influence the gonadal development and spawning of this species, have been plotted for each of those 4 years (Fig. 1). This facilitates the pattern of gonadal development and estimated time of spawning in 1978/1979 to be considered in the context of data on seasonal changes in environmental variables gathered over a far longer period than that encompassed by the present study.

A total of 19 larvae, caught between November and March of 1986 and 1987 at sites in the upper Swan Estuary, were used to describe the early development of *A. caudavittata*. All larvae were caught at night, using conical plankton nets (500-μm mesh), during monthly sampling of ichthyoplankton throughout the Swan Estuary [see Neira *et al.* (1992) for details].

The body length (B.L.) of each *A. caudavittata* larva, i.e. notochord length in pre-flexion and flexion larvae and the standard length in post-flexion larvae, was measured to the nearest 0·1 mm using a stereomicroscope fitted with an eyepiece micrometer.

LENGTHS, WEIGHTS AND TREATMENT OF GONADS

All fish were measured (total length) to the nearest 1 mm and weighed to the nearest 100 mg, except when the sample contained large numbers of the discrete groups of small and larger fish, in which case a subsample of 100 representatives of each of these two size classes were randomly selected for the measurement of lengths and weights. The sex of each fish was recorded, except in the case of those small fish where the identity of the gonad could not be determined. The sagittal otoliths were removed and whether they had zero or one or two clearly defined translucent zones was recorded. Note that, while the first two translucent zones have been validated as corresponding to annuli, a marked change in the growth of these otoliths during the third year of life makes it difficult subsequently to determine which of the later translucent zones in the otoliths of older fish correspond to annuli (Wise *et al.*, in press). The GSIs for all older fish, which are clearly identifiable in length–frequency data (Wise *et al.*, in press), are thus grouped in the Results and in Fig. 2 under the category of fish with two annuli.

In each month, gonads were removed from random subsamples of the groups of fish with otoliths having one and two well-defined translucent zones. The gonad of each fish was weighed to the nearest 1 mg and the gonadosomatic index (GSI) calculated from the equation $W_1/W_2 \times 100$, where W_1=wet weight of gonad and W_2=wet weight of fish in the same units. The ovaries were fixed in Bouin's fluid and stored in 70% ethanol. The staging of ovaries as developing (III), maturing (IV), mature (V), spawning (VI), spent (VII) and recovering spent or resting (VIII) follows the criteria of Laevastu (1965). Segments of the mid-region of several ovaries from each month were examined under a dissecting microscope and the diameters of at least 100 of those oocytes whose diameters were greater than 100 μm were measured to the nearest 10 μm.

The fecundities of 23 sexually mature females, representing the full range of lengths of mature female fish (150 to 285 mm), were estimated by extrapolating from the numbers counted in subsamples of known weight to the total weight of the ovary.

III. RESULTS

ENVIRONMENTAL VARIABLES

Day length in the region of the Swan Estuary declined in each year from *c.* 840 min in January to a minimum of *c.* 600 min in June, and then rose

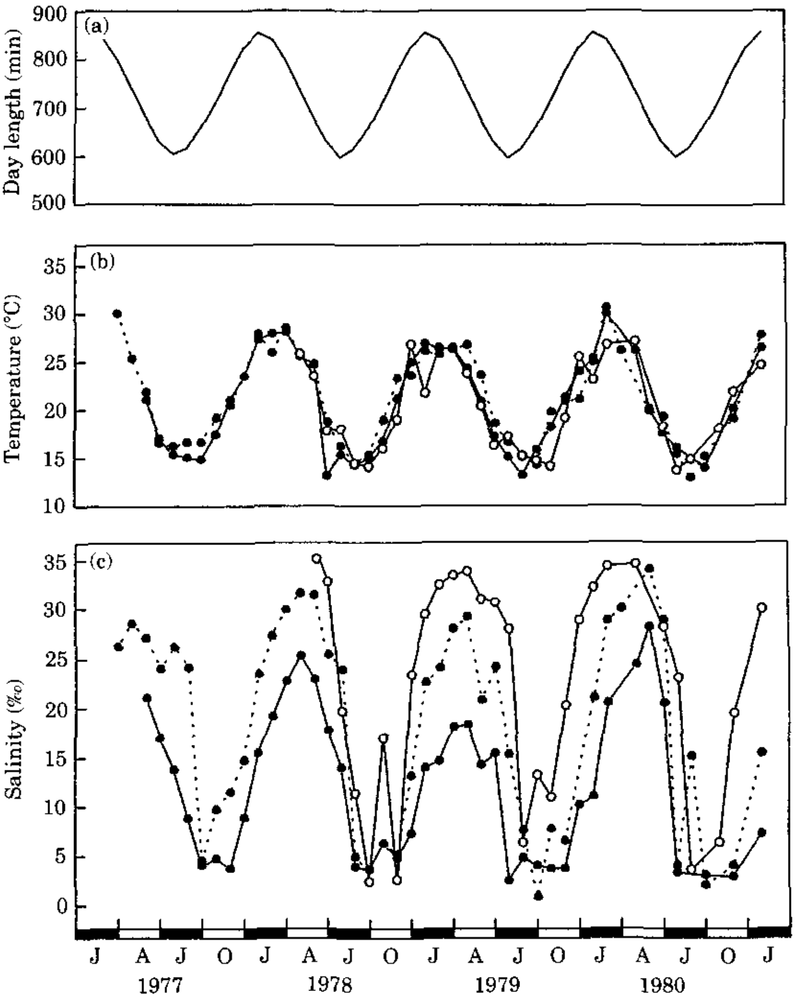

FIG. 1. (a) Day length, (b) water temperature and (c) salinity at Sites 5 and 6 in the Swan River and at Site 9 the Canning River. On the horizontal axis of this figure and Fig. 2, the closed rectangles represent the summer and autumn months and the open rectangles the autumn and spring months. Site 6 ●——●; Site 5 ● · · · ●; Site 9 ○——○. Note that data for Site 9 were only collected from March 1978.

progressively to *c*. 770 min in October and then to a maximum of *c*. 850 min in December (Fig. 1).

Water temperatures at Site 6 followed very similar trends in each year, rising progressively from their minima of 13–15° C in July to 20–21° C in October and then to their maxima of 26–30° C in February (Fig. 1). They subsequently fell quite markedly during the autumn and early winter. The monthly water temperatures at Sites 5 and 9 in each month were very similar to those at Site 6.

Although salinity showed similar and marked seasonal trends to those of temperature, the phasing was slightly later (Fig. 1). Thus, salinity in the upper estuary did not start rising sharply until November and did not peak until March. Salinities at Site 6 were low between July (3·9–8·8‰) and October (2·9–4·8‰),

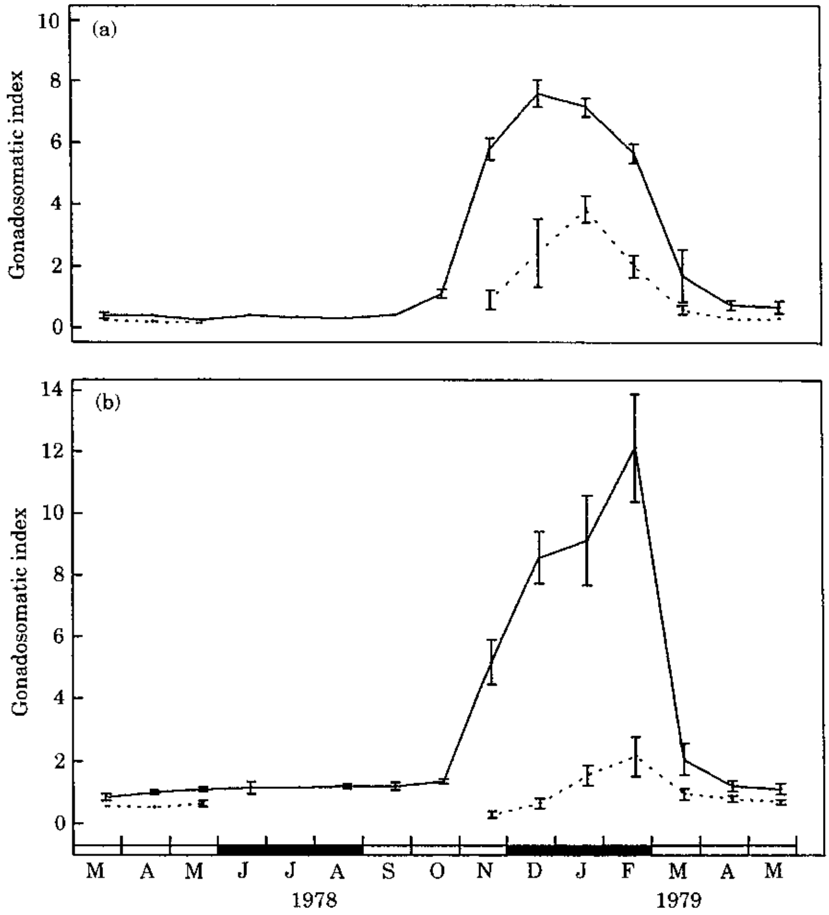

FIG. 2. Mean gonadosomatic indices ± 95% confidence limits for sequential monthly samples of (a) male and (b) female *Amniataba caudavittata* with otoliths having one (- - -) and two (——) well-defined annuli. Sample sizes of these two groups were almost invariably greater than 10 in each month and were usually over 30 in the months between mid-spring and early autumn.

but then rose sharply to 15–21‰ in January and 18–25‰ in March (Fig. 1). Salinities were consistently greater at Site 5 and even more particularly at Site 9 than at Site 6. Thus, in November, mean salinities had already reached *c.* 14‰ at Site 5 and 26‰ at Site 9, compared with only *c.* 9% at Site 6. By December, the means at these three sites were *c.* 21, 31 and 12‰, respectively (Fig. 1).

Trends shown by gonadal and oocyte development

The monthly mean GSIs of the group of males, whose otoliths had two annuli, rose sharply in 1978 from less than 0·4 between July and September and 1·1 in October, to 5·8 in November and 7·5 in December (Fig. 2). They remained at *c.* 7 in January 1979, before declining to 5·6 in February and then falling precipitously to 1·6 in March and 0·7 in May. The mean monthly GSIs of the comparable group of females followed similar trends to those of males, except that the maximum (12·1) was attained later, i.e. in February 1979 rather than in

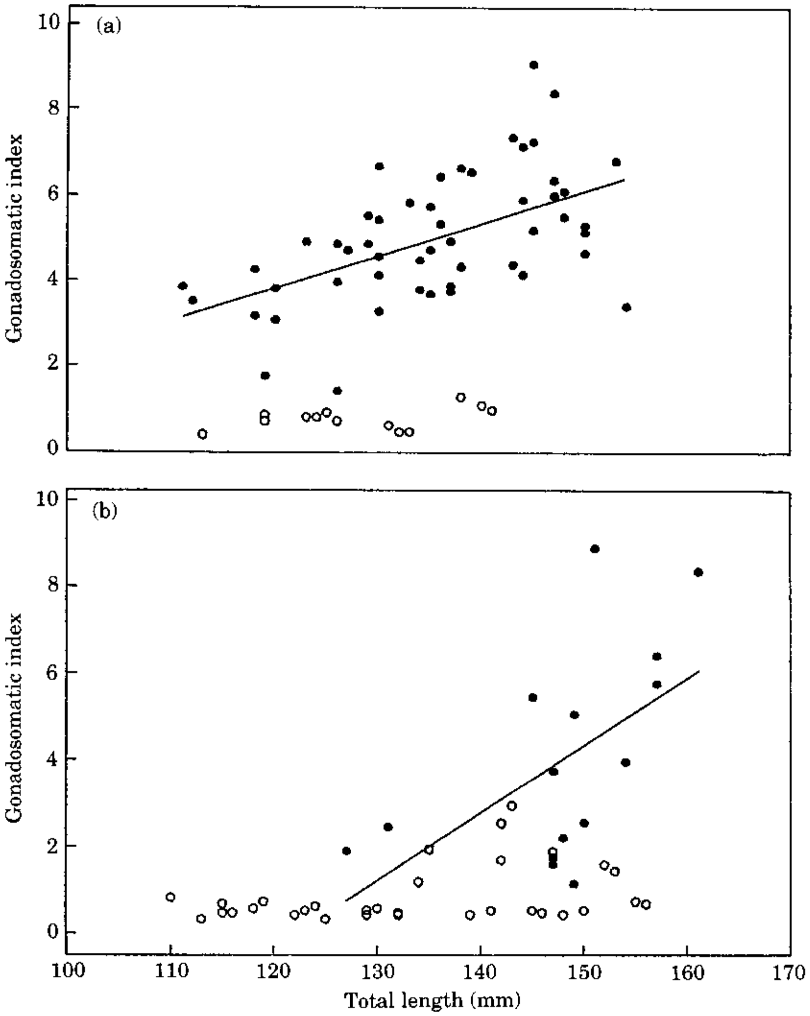

FIG. 3. The relationships between gonadosomatic index and total length of 1-year-old (a) male and (b) female *Amniataba caudavittata* from Sites 5 and 6 (●) and Site 9 (○) in the Swan Estuary January 1979.

December 1978 (Fig. 2). However, the mean GSI of females underwent a very similar marked decline between February and March of 1979 to that exhibited by the GSI of males.

Although the mean GSIs of both the male and female fish with otoliths having one annuli followed similar seasonal trends to those described above, they were always far lower in any given month (Fig. 2).

The magnitude of the GSIs of individuals comprising the cohort of males and females with otoliths having one annuli was related to both the size of fish and the location of capture. Thus, at Sites 5 and 6 in the Swan-Avon River, the maximum GSIs of male fish in January 1979 rose from 4·3 in fish less than 120 mm to 6·6 in fish of 120 to 139 mm and 9·0 in those over 140 mm (Fig. 3). In contrast, the maximum GSIs of male fish caught at Site 9 in the lower reaches of

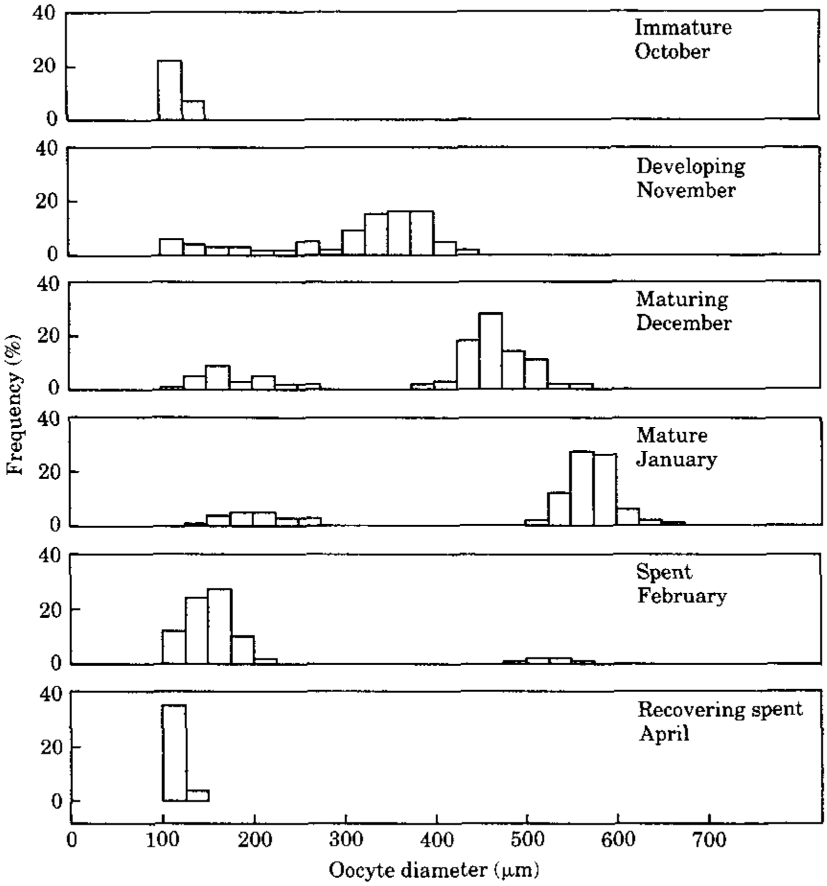

FIG. 4. Frequency histograms for the diameters of oocytes >100 in sequential stages of ovarian development.

the Canning River, and measuring between 112 and 141 mm, never exceeded 1·1. Although a similar situation to that described above for males was also recorded for females, the prevalence of females with elevated GSIs (>3·5) was not as high.

The linear relationships between the GSI and total length of the male and female fish at sites 5 and 6 shown in Fig. 2 are expressed by the following equations:

$$\text{males GSI} = -5{\cdot}21 + 0{\cdot}08\ \text{T.L.}\ (n=51,\ r^2=0{\cdot}29,\ P<0{\cdot}001)$$

$$\text{females GSI} = -18{\cdot}9 + 0{\cdot}16\ \text{T.L.}\ (n=15,\ r^2=0{\cdot}32,\ P<0{\cdot}05)$$

Pressure applied to the abdomen of the female and male fish with the highest GSIs resulted in the extrusion of eggs and milt, respectively.

The changes in the typical distribution of oocyte diameters in sequential stages of ovarian development at different times of the year demonstrate that the sharp increase that occurred in the mean GSIs of females between October and January, reflected a progressive and marked increase in the size of a proportion of the oocytes in the ovary (Fig. 4). Thus, whereas the diameters of all oocytes

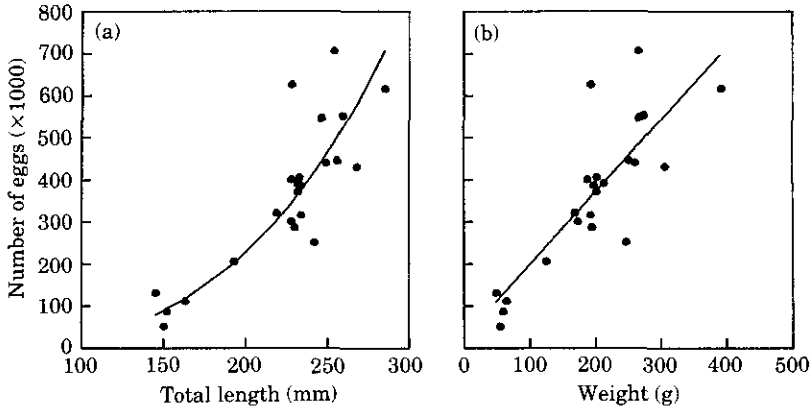

FIG. 5. The relationships between the number of eggs and (a) the length and (b) weight of mature *Amniataba caudavittata*.

were less than 150 µm in immature (Stage III) ovaries in October, some of these oocytes had developed into a conspicuous group of large oocytes in developing (Stage IV) ovaries in November and this had become discrete in maturing (Stage V) ovaries in December and remained so in mature ovaries (Stage VI) in January (Fig. 4). The modal diameter class of the larger oocytes in the mature ovary was 550–574 mm, which is appreciably greater than the 450–474 mm recorded in the maturing ovary. Although a few large oocytes were still present in the recently spent ovary from February, they were no longer present in a recovering spent ovary taken from a fish in April (Fig. 4).

The number of mature eggs in the ovaries of 23 fully mature females ranged from 50 000 in a 150-mm fish to 705 000 in a 254-mm fish. The mean ± 95% confidence limits for these fish was 310 000 ± 82 000. The relationship shown in Fig. 5 between the number of eggs (F) and the total length and weight of these fish can be expressed by the following equations:

$$\log F = -2{\cdot}08 + 3{\cdot}23 \log \text{T.L.} \; (n=23,\ r^2=0{\cdot}84,\ P<0{\cdot}001)$$

$$F = 25\,322 + 1712\ W \; (n=23,\ r^2=0{\cdot}69,\ P<0{\cdot}001)$$

The mean diameter ± 95% confidence limits of 142 fully mature eggs obtained from preserved mature ovaries was 560 ± 5·9 µm.

Spawning period and estimation of the birth date

The aforegoing data can now be employed to help estimate the duration of spawning and when it peaks. The latter value is crucial for providing a reliable birth date that can be used for determining von Bertalanffy growth curves (Wise *et al.*, in press).

The following information demonstrates that spawning occurs between the end of spring and end of summer. First, the mean GSIs of both males and females with otoliths having two clearly defined annuli rose sharply between October and November of 1978 and then remained high between December 1978 and early February 1979, but with considerable variability in the individual values of particularly the females, and then fell precipitously in March. Second,

TABLE I. Range in body lengths and body intervals recorded for larval *Amniataba caudavittata* from the upper Swan Estuary

Stage	*n*	Body length (mm)	Head length	Pre-anal length	Body depth at pectoral fin base
Pre-flexion	4	4·1–4·8	18·6–18·7	30·0–31·2	11·6–16·7
Flexion	3	4·9–5·2	17·3–20·4	30·8–33·6	15·4–17·3
Post-flexion	12	5·6–7·8	21·9–29·8	38·6–46·7	17·2–23·1

Body intervals are expressed as a percentage of body length.

recently-spent ovaries were found only between mid-November 1978 and early February 1979. Third, the 0+ recruits first appeared as juveniles in January in both 1978 and 1979 (Wise *et al.*, in press). Fourth, the 31 larvae of *A. caudavittata* obtained during extensive monthly sampling of ichthyoplankton throughout the Swan Estuary were all collected between November and March, and predominantly in January (Neira *et al.*, 1992; Neira, personal observation). From the above data, it can also be concluded that spawning activity peaks in late December/early January, and that it is thus appropriate to assign a birth date of 1 January to the members of the *A. caudavittata* population in the Swan Estuary. Since the modal length of the 0+ recruits was sharply defined (Wise *et al.*, in press), most of the spawning would have occurred in a relatively restricted period around that time.

DEVELOPMENT OF LARVAE

Identification of larvae

Larvae were identified as belonging to the Terapontidae by their elongate body, short and coiled gut and the presence of preopercular spines and 25 myomeres (Leis & Trnski, 1989). The pattern of body pigmentation and the degree of fin development were used to assemble the larvae into a series. Postflexion larvae were identified as those of *A. caudavittata* by the dorsal and anal fin counts of XIII, 9 and III, 8 respectively (Vari, 1978; Leis & Trnski, 1989). This identification was further supported by the fact that all of the larvae used for this description were caught in the upper reaches of the Swan Estuary where no other terapontids are found (Loneragan *et al.*, 1989).

Development of larvae

The larvae of *A. caudavittata* are characterized by an elongate body, which becomes moderately deep and laterally compressed during development, a short to moderate, tightly-coiled and compact gut, a distinct gap between the anus and the origin of the anal fin and the presence of 25 or 26 myomeres (Fig. 6). The smallest larva illustrated (4·1 mm) has a short and coiled gut, pectoral fin buds, a continuous dorsal and anal fin fold and no trace of a yolk sac [Fig. 6(a)]. Notochord flexion commences by 4·9 mm and is complete by 5·2 mm (Table I).

The relative length of the head increases from about 18% B.L. in pre-flexion larvae to nearly 30% B.L. in post-flexion larvae (Table I). The mouth reaches the

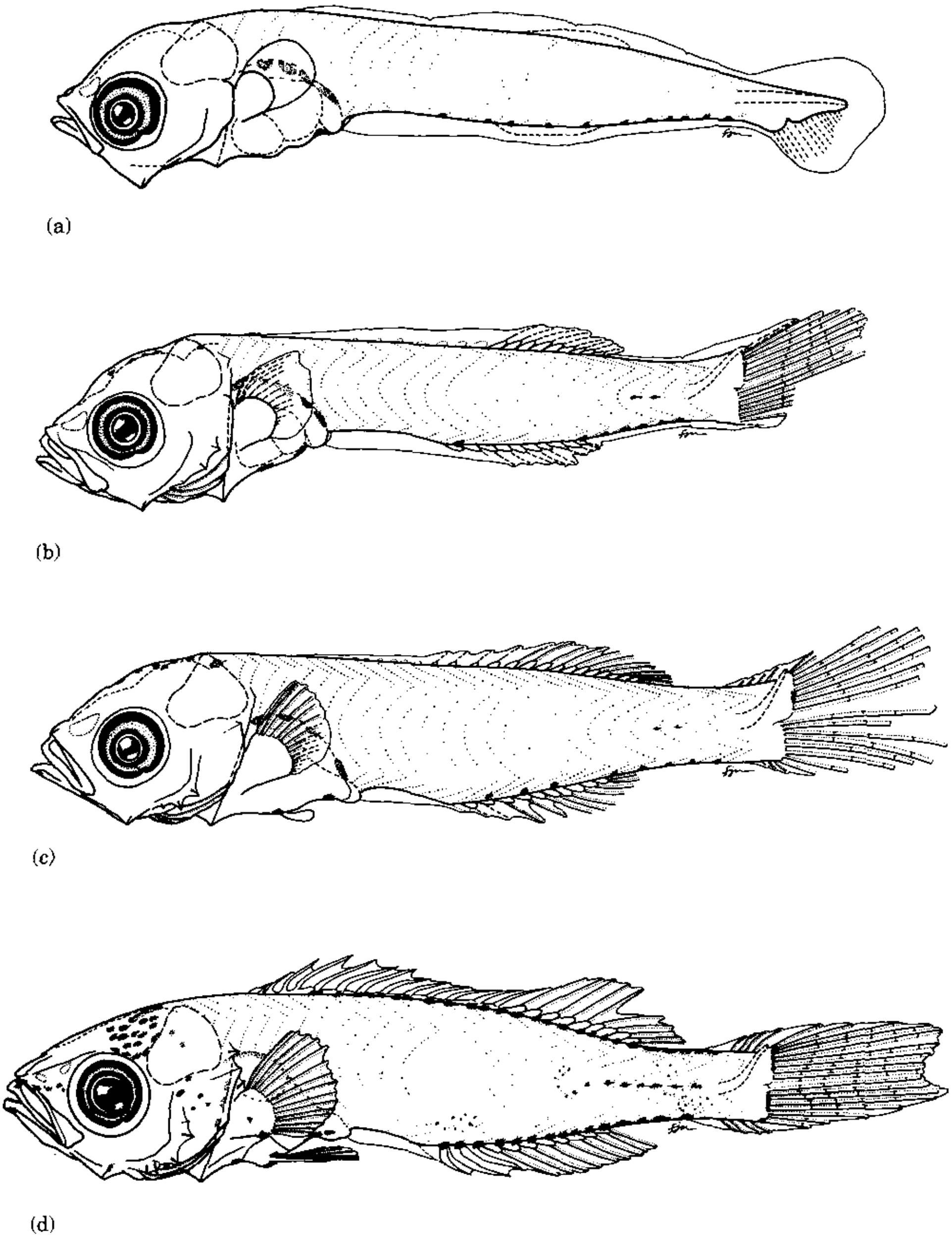

FIG. 6. Larvae of *Amniataba caudavittata* illustrated from specimens caught in the upper Swan Estuary. (a) 4·1 mm B.L. pre-flexion larva; (b) 5·1 mm B.L. late flexion larva, (c) 5·6 mm B.L. early post-flexion larva and (d) 6·6 mm B.L. post-flexion larva.

anterior edge of the eye in all larvae. Small villiform teeth have formed on the premaxilla and dentary by 4·9 mm and two to three small spines are present along the posterior margin of the preoperculum by 5·1 mm [Fig. 6(b)]. The number of pre-opercular spines increases to five in 6·6-mm larvae and the preoperculum becomes finely serrated in larvae over 7·7 mm. Cleithral, opercular and supracleithral spines form in larvae over 6·4 mm [Fig. 6(d)].

The pre-anal distance increases from 30–31% B.L. in pre-flexion larvae to 39–47% B.L. in post-flexion larvae (Table I). The distinct gap, which remains between the anus and the origin of the anal fin throughout development, has a post-anal membrane which remains in post-flexion larvae [Fig. 6(d)]. A small, pigmented gas bladder is visible over the anterior part of the gut in all stages of development.

Fin development

The rays of the caudal fin begin to form just prior to flexion and all (9+8) rays are developed by 5·2 mm. The soft rays of the second dorsal and anal fins appear simultaneously by 4·9 mm, i.e. when flexion has commenced. The spines of both the first dorsal and anal fins start to develop by 5·6 mm and all spines and rays in the dorsal (XIII, 9) and anal (III, 8) fins are present by 6·6 mm [Fig. 6(d)]. The third spine of the anal fin is initially a soft ray and becomes a spine by 5·7 mm. The rays of the pectoral fins start to form sequentially from dorsal to ventral by 5·0 mm and all (15–17) rays are formed by 6·6 mm. Buds of the pelvic fins appear in 5·6 mm larvae and all (I, 5) rays are formed by 6·6 mm [Fig. 6(d)].

Pigmentation

The larvae of *A. caudavittata* are lightly pigmented before settlement. The head is unpigmented in pre-flexion larvae. Melanophores form on the midbrain during flexion. Two melanophores form at the tip of the lower jaw, one at the angle of the lower jaw and several on the operculum in post-flexion larvae. Pigment is present over the dorsal surface of the gas bladder and gut in the smallest larva examined and intensifies in this region during development. A ventral melanophore is present just in front of the anus of pre-flexion larvae. Another melanophore appears at the centre of the ventral surface of the gut just before flexion has commenced and another forms posterior to the cleithral symphysis in post-flexion larvae (Fig. 6).

A single row of 8–11 melanophores is present along the ventral surface of the tail in pre-flexion larvae. This row becomes double along the base of the anal fin and remains single along the ventral surface of the caudal peduncle in post-flexion larvae (Fig. 6). Shortly before flexion is complete, melanophores form laterally on the caudal peduncle and on the upper caudal fin base. A single row of melanophores appears dorsally on the caudal peduncle by 6·4 mm and extends along the base of the dorsal fin by 6·6 mm. Pigment extends over the whole trunk and the posterior area of the tail of larvae over 6·6 mm. Internal melanophores develop in the snout and along the cleithrum in post-flexion larvae over 6·4 mm (Fig. 6).

IV. DISCUSSION

AGE AND SIZE AT MATURITY AND FECUNDITY

Since the annulus on the otolith of *A. caudavittata* becomes delineated by November (Wise *et al.*, in press), this is formed in each year just over 2 months prior to the birth date of 1 January. Thus, fish with otoliths having a single annulus in November and December are in the last 2 months of their first year of life. However it was not possible to determine the precise number of annuli on the otoliths of the oldest fish, i.e. on those otoliths with two translucent zones that are clearly detectable, but which may contain one or more additional, ill-defined annuli (see Materials and Methods). Thus, the group of fish with otoliths having two such zones comprises all older fish, commencing with those which in November were approaching the end of their second year of life.

The high values attained by the GSIs of virtually all male and female *A. caudavittata* that possessed otoliths with two clearly defined annuli indicate that, in general, all members of this species attain sexual maturity at the end of their second year of life, and that this applies also to fish of older age classes. Such a conclusion is supported by the observation that, in December and January, virtually all of the ovaries of these fish were at stages V (mature), VI (spawning) or VII (spent). However, the presence of high GSIs and mature gonads in some of the fish with otoliths having one annulus show that maturity is also sometimes reached at the end of the first year of life. This occurred more frequently with male than female fish. It is also clear from our data that 1-year-old male and female fish are unlikely to become mature unless they are at least 130 and 150 mm in length, respectively. The above results conflict markedly with the statement of Thompson (1957) that *A. caudavittata* reaches maturity at ' age IV '. The minimum lengths of females recorded during the present study are also lower than those given by Thompson (1957), both overall (244 *v.* 282 mm) and at maturity (150 *v.* 204 mm).

Spawning location

The fact that sexually mature fish were caught predominantly at Sites 5 and 6 in the upper Swan Estuary suggests that spawning occurs mainly in that part of the system. Such a view is consistent with the observation that in 1978, the year when recruitment was greatest, all but one of the 309 0+ recruits caught in January, the month when recruitment first occurred, were collected from sites in the upper estuary. It is also consistent with the fact that virtually all *A. caudavittata* larvae caught during extensive sampling of ichthyoplankton throughout the Swan Estuary came from its upper region (Neira *et al.*, 1992). Since the catches taken in seine nets in the summer were far greater than at other times of the year, whereas the reverse situation pertained with those taken in otter trawls and gillnets (Wise *et al.*, in press), spawning presumably takes place in the shallow waters near the shore.

Factors influencing gonadal development and spawning time

Since gonadal development in *A. caudavittata* accelerated between October and December/January, as day length and water temperature were rising markedly, gonadal recrudescence in this species may well have been stimulated by increases in these variables. Such a conclusion would be consistent with the abundance of field and environmental data which support the view that increases in these variables are the most important of the environmental trends responsible for stimulating gonadal recrudescence in teleosts in temperate waters (Lam, 1983; Bye, 1984). However, since day length and water temperature in the Swan Estuary were already rising in August, whereas conspicuous gonadal recrudescence did not start until salinity had also started to rise in November, this latter environmental variable may also play a role in stimulating gonadal development.

The spawning of *Leiopotherapon unicolor* (Günther) and that of another freshwater terapontid, *Bidyanus bidyanus* (Mitchell), are stimulated by flooding (Lake, 1967*a*; Llewellyn, 1973; Beumer, 1979). However, since freshwater discharge in the Swan Estuary declines progressively during the spring and summer, the environmental stimulus for *A. caudavittata* to spawn must be some variable other than flooding. Since Lam (1983) has concluded that water temperature was the most important of the environmental variables in initiating spawning, it is worth noting that spawning commenced in November, when the water temperature was *c.* 24° C, and that it peaked when it was *c.* 27° C.

The fact that in January 1979 1-year-old fish in the Canning River always had low GSIs and never reached maturity demonstrates that gonadal recrudescence had not been stimulated in this region of the estuary. Since the light and temperature regimes in this part of the system were very similar to those in the Swan-Avon River, where these fish exhibited gonadal development and occasionally attained maturity, some other stimulating factor must have been absent in the Canning River. Although food availability can influence gonadal development (Bye, 1984), an examination of length/weight relationships showed that, if there was insufficient food to initiate gonadal recrudescence in young fish in the Canning River, it did not result in a lower condition factor [*sensu* Ricker (1975)] in the fish of this region than in those of the Swan-Avon River. It may be significant, however, that salinities started to rise earlier at the site in the Canning River than in the Swan-Avon River. Thus, the salinity cue for the initiation of gonadal development may have occurred too early for the 0+ fish in the Canning River to respond.

Egg size and fecundity

The mean diameter of the unfertilized mature eggs of *A. caudavittata* recorded in the present study (560 µm) is similar to that given by Thompson (1957) for this species and by Miu *et al.* (1990) for the marine species *Terapon jarbua*. While this diameter is only slightly less than that of *L. unicolor*, it is approximately half that of *B. bidyanus* (Lake, 1967*b*; Beumer, 1979).

The maximum fecundity of 705 000 recorded for *A. caudavittata* in the present study is nearly an order of magnitude greater than the maximum fecundity of 72 250 given by Thompson (1957). Our mean fecundity of 310 000 is far more in line with the fecundity of *c.* 500 000 estimated by Lenanton (personal communication) for *A. caudavittata* in Shark Bay, a large marine embayment approximately 750 km to the north of the Swan Estuary. The high fecundity of *A. caudavittata* is a characteristic of the Terapontidae in general (Beumer, 1979; Miu *et al.*, 1990), and is regarded by Beumer (1979) as reflecting a large production of eggs by the marine ancestors of this family.

LARVAL DEVELOPMENT

Development in the Terapontidae

The only larvae of terapontid species that have been described are those of the freshwater species *Bidyanus bidyanus* and *Leiopotherapon unicolor* (Lake, 1967*a,b*; Llewellyn, 1973), and of the marine species *Pelates sexlineatus* (Quoy & Gaimard) (Munro, 1945), *P. quadrilineatus* (Bloch) (Miskiewicz, 1987), *Rhyncopelates oxyrhynchus* (Temminck & Schlegel) (Kinoshita, 1988), and *Pelates* sp., *Terapon theraps* (Cuvier) and *T. jarbua* (Zvjagina, 1965; Kinoshita, 1988; Leis & Trnski, 1989).

The morphology of the larvae and the size at which ontogenetic changes occur during larval development varies considerably amongst the different species of terapontids (Leis & Trnski, 1989). For example, in comparison with the larvae of *Terapon*, those of *Amniataba*, and also of *Pelates*, have a more elongated body, less developed spination on the head and a greater gap between the anus and the origin of the anal fin (cf. this study; Kinoshita, 1988; Leis & Trnski, 1989). In addition, all fins in *A. caudavittata* larvae are completely formed at a smaller size than in the larvae of other terapontid species. Thus, while all of its fins have been formed in *A. caudavittata* by 6·6 mm, they are not formed until between 8·0 and 12·3 mm in *P. quadrilineatus* and *T. theraps*, and until over 12·5 mm in *B. bidyanus* and *c.* 20·0 mm in *L. unicolor* (Lake, 1967*a,b*; Llewellyn, 1973; Miskeiwicz, 1987; Leis & Trnski, 1989). The weak head spination of larval *A. caudavittata*, a feature retained by the adults, appears to be the only specialization of these larvae to pelagic life. Since only a few post-flexion *A. caudavittata* larvae were caught in the upper Swan Estuary, the larvae of this species presumably settle shortly after the fins are fully formed, i.e. at lengths <8·0 mm and thus well below the lengths of at least 12 mm at which this occurs in *T. theraps, T. jarbua* and *P. sexlineatus* (Munro, 1945; Leis & Trnski, 1989; Neira, unpublished data).

OTHER TERAPONTIDS IN THE SWAN ESTUARY

Two other terapontids, *Pelates sexlineatus* and *Pelsartia humeralis* (Ogilby), are found in the Swan Estuary (Chubb *et al.*, 1979). However, the larvae and juveniles of the former are found mainly in the lower reaches of the Swan Estuary (Neira *et al.*, 1992), while the latter is a marine species whose adults have been recorded on only a few occasions and then only in the lower Swan Estuary (Loneragan *et al.*, 1989). The larvae of *P. sexlineatus* can be distinguished from those of *A. caudavittata* by the dorsal and anal fin counts of XII, 10 and III, 10 respectively, and by the presence of a row of internal melanophores along the dorsal surface of the notochord (Neira, unpublished data).

COMPARISONS OF REPRODUCTIVE STRATEGIES IN SOUTH-WESTERN AUSTRALIAN ESTUARIES

A. caudavittata is one of the 14 teleost species which were recorded by Loneragan *et al.* (1989) as being able to complete their life cycles within the Swan Estuary. Recent work by Laurenson *et al.* (1993) has shown this list should now also include the plotosid *Cnidoglanis macrocephalus* (Cuvier & Valenciennes). Moreover, the clupeid *Nematalosa vlaminghi* (Munro), which spends much of its life feeding at sea, also spawns within the Swan Estuary (Chubb & Potter, 1984). From the data presented in Loneragan *et al.* (1989), it can thus be calculated that approximately 65% of the fish caught in seine nets and 75% of those taken in gillnets in the Swan Estuary belong to species that breed within this estuary.

The importance of the Swan Estuary, and also other south-western Australian estuaries such as the Peel-Harvey Estuary and Wilson Inlet, as a spawning area for teleosts (see also Loneragan *et al.*, 1986; Potter *et al.*, 1990, 1993; Neira & Potter, 1992), contrasts markedly with the situation in estuaries in temperate regions of the Northern hemisphere, where the fish faunas are dominated by marine species (Haedrich, 1983; Dando, 1984; Claridge *et al.*, 1986; Kennish, 1990). It has been suggested that the considerable number of species that are capable of spawning in south-western Australian estuaries reflects adaptations to the seasonal or longer periods of landlocking to which these estuaries have been subjected in the past and to which, in many cases, they are still being exposed (Potter *et al.*, 1986, 1990, 1993).

It is also important to recognize, however, that the combination of the small tidal range and low rainfall found in south-western Australia in the late spring and summer (Hodgkin & Lenanton, 1981), means that conditions in the estuaries of this region at that time are relatively stable. Since that is the period when teleosts, such as *A. caudavittata*, *N. vlaminghi*, *Acanthopagrus butcheri* (Munro), *Engraulis australis* (Shaw) and *Platycephalus speculator* (Klunzinger), are spawning (Chubb & Potter, 1984; Chrystal *et al.*, 1985; Hyndes *et al.*, 1992; Neira *et al.*, 1992), their eggs and larvae are not exposed to the effect of strong tidal action and marked freshwater discharge that often characterize temperate estuaries in the Northern Hemisphere. The stability of south-western Australian estuaries is of particular importance to these species, since their eggs are pelagic and their larvae are poorly developed at hatching. At the same time, any tendency for mortality to be high will be compensated for by the very high fecundity of these species. The fact that environmental stability even extends at that time into the riverine upper estuary, where freshwater discharge would otherwise be most likely to exert a flushing effect, helps account for the very high percentage contribution (85%) that the numbers of fish larvae collected in that part of the system made to the total catch of fish larvae obtained by Neira *et al.* (1992) from sites throughout the Swan Estuary.

In contrast to the above five species, the majority of the species that spawn in typical temperate Northern Hemisphere estuaries produce demersal or non-buoyant eggs, a characteristic that would reduce the likelihood of their being flushed out of the system (Dando, 1984). Demersal and adhesive eggs are produced, however, by members of the Atherinidae, Gobiidae and Blenniidae in south-western Australian estuaries, where their breeding occurs over a long period and commences in the spring when freshwater discharge is still appreciable (Prince & Potter, 1983; H. S. Gill, in preparation). Although the larvae of these three families are not well developed at hatching, and thus susceptible to the flushing action in estuaries in the spring, it is relevant that, because of their protracted spawning, these species also produce many larvae during the summer when conditions are far more stable. Furthermore, gobiids and bleniids produce large numbers of small adhesive and demersal eggs, which results in at least some surviving under harsher conditions. Although small eggs are also produced by the members of the Syngnathidae, these are guarded by the males in their pouches. The cardinal fish *Apogon rueppellii* (Günther) and *C. macrocephalus*, which, like the above species, are abundant in the estuaries of south-western Australia (Loneragan *et al.*, 1989), produce a small number of large eggs, exhibit parental care and have larvae that are well developed at hatching (Chrystal *et al.*, 1985; Neira, 1991; Laurenson *et al.*, 1993). There is thus a wide spectrum of reproductive strategies exhibited by the species that complete their life cycles in these estuaries which, in most cases, have resulted in large numbers of individuals being produced by these species in some years.

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