Abstract–Age compositions and growth rates have been determined for populations of *Acanthopagrus butcheri* in four estuaries and a saline, coastal lake, all of which differ markedly in their morphological, physicochemical, and biotic characteristics. Because the opaque zones in otoliths were shown to form annually, the number of these zones could be used to age individual fish. However, the otoliths of fish that were more than six years old had to be sectioned in order to consistently reveal all opaque zones. The number of annuli on scales did not provide reliable estimates of age. *Acanthopagrus butcheri*, which typically completes its life cycle in estuaries, was represented in each of the five water bodies by fish ≥15 years old and lengths and weights >365 mm and >860 g, respectively. The maximum length and weight of *A. butcheri* recorded in any of the five water bodies were 485 mm and 2196 g, respectively. The values for L_∞ in von Bertalanffy growth equations differed significantly between females and males in three of the four estuarine populations ($P<0.001$ or <0.01), whereas those for both k and t_0 differed significantly between the sexes in only one population and then only at $P < 0.05$. The values for k and L_∞ in the von Bertalanffy growth equations differed significantly among both females and males in the four estuaries at either $P < 0.001$ or $P < 0.05$. These parameters also differed significantly between the males in Lake Clifton and the males in each estuary, except the Swan River Estuary. Growth rates in two of the more northern water bodies were greater than those in the two southern and cooler estuaries. The pattern of growth in the Moore River Estuary, as reflected by changes in length with time, differed from that in the other four water bodies in that it was initially slower and subsequently did not show such a marked tendency to form an asymptote. The slow initial rate of increase in length in the Moore River Estuary may be related to particularly high densities of juvenile *A. butcheri* in nearshore, shallow water, as well as to a relatively lower abundance of appropriate food or very low salinities, or to both of the latter. The percentage contribution made by fish ≥5 years was the lowest by far in the Swan River Estuary, which was subjected to the greatest fishing pressure.

Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors

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The black bream, *Acanthopagrus butcheri*, which completes its life cycle within estuaries (Potter and Hyndes, 1999; Sarre and Potter, 1999) is one of the most important recreational and commercial fish species in the estuaries of southern Australia (Lenanton and Potter, 1987; Kailola et al., 1993). The fact that the genetic compositions of the populations of this species in the different estuaries of southwestern Australia vary, suggests that, although some *A. butcheri* are occasionally flushed out of estuaries during those winters when freshwater discharge is particularly heavy, the population in an estuary remains essentially discrete from those in other estuaries (Chaplin et al., 1998; Potter and Hyndes, 1999). The confinement of each population of *A. butcheri* to its natal environment means that, if fishing pressure is sufficiently high in any one estuary, the population in that estuary cannot be replenished naturally by immigration from outside that system. Indeed, there is good evidence that the abundance of this sparid in the Blackwood River Estuary in southwestern Australia declined markedly between the 1970s and 1990s as a result of a combination of commercial and recreational fishing activities (see Valesini et al., 1997; Lenanton et al., 1999; Lenanton[1];Valesini[2]).

The increasing potential for *A. butcheri* to become overexploited as recreational fishing in estuaries increases means that it is now important to have information on the age compositions of this species in the various estuaries in order to ascertain whether the older age classes are becoming excessively depleted in some of these estuaries.

Such data are dependent on accurate estimates of the age of fish. In the past, such estimates for *A. butcheri* have typically been based on the number of annuli on scales (Butcher, 1945; Thomson, 1957; Weng, 1971; Hobday and Moran[3]). However, no attempt was made in any of these studies to use traditional methods to validate that the growth zones (annuli) on that hard structure are formed annually—a procedure now considered essential in aging fish (Beamish and McFarlane, 1983). Although Morison et al. (1998) have recently used the number of opaque zones on otoliths as a criterion of age, their approach to validating that those zones were formed annually was based on the observation that the number of opaque zones on the otoliths of fish in the two cohorts that were the most strongly represented in length-frequency data for four consecutive years increased by one in each successive year.

Recent work on *A. butcheri* in southwestern Australia has focused on populations in four estuaries and a landlocked saline, coastal lake, which vary

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[1] Lenanton, R. C. J. 1977. Aspects of the ecology of fish and commercial crustaceans of the Blackwood River Estuary, Western Australia. Report 19, Department of Fisheries and Wildlife, Perth, Western Australia, Australia, 72 p.

[2] Valesini, F. J. 1995. Characteristics of the ichthyofaunas of the Blackwood River Estuary and Flinders Bay. Unpublished honours thesis, Murdoch University, Perth, Western Australia, Australia, 67 p.

[3] Hobday, D., and Moran, M. 1983. Age, growth and fluctuating year class strength of black bream in the Gippsland Lakes, Victoria. Report No. 20. Marine Science Laboratories, Victoria, Australia, 17 p.

markedly in their morphological and physicochemical characteristics and in the composition of their biota (Sarre et al., 2000). Thus, two of these water bodies are permanently open to the sea, while one is intermittently closed, another is normally closed, and one is permanently closed. Furthermore, the regions where *A. butcheri* spawns in these estuaries in the spring and early autumn range in salinity from as low as 3.5–8.0‰ in the intermittently open estuary to over 40‰ in the normally closed estuary and, as a result of their location at different latitudes, they also differ in water temperature (Young et al., 1997; Sarre and Potter, 1999). The differences in the biota of these systems are reflected in marked differences in the dietary composition of *A. butcheri*, with, for example, the overall contribution made by macrophytes to the volume of stomach contents ranging from as low as 8.3% in one population to as high as 56.4% in another (Sarre et al., 2000).

The aims of our study on *A. butcheri* were as follows: 1) to validate that the growth (opaque) zones visible on sectioned otoliths of *A. butcheri* are formed annually; 2) to compare the number of growth (opaque) zones in otoliths prior to and after sectioning in order to determine whether otoliths always have to be sectioned to reveal each of their opaque zones; 3) to ascertain whether the number of annuli on scales corresponds to the number of opaque zones on sectioned otoliths and can thus likewise be used for aging this species; 4) to determine the age composition of *A. butcheri* in the above four estuaries and the saline, coastal lake, in which the fishing pressure on black bream varies from zero to substantial, and thereby ascertain whether there is evidence that heavy exploitation of this species can markedly reduce the proportion of older fish; and 5) to determine the extent to which the growth rates and length at age of *A. butcheri* differ amongst populations in the above five water bodies, which vary markedly in their abiotic and biotic characteristics and amongst which the dietary compositions of *A. butcheri* are significantly different.

Materials and methods

Acanthopagrus butcheri was collected from the permanently open Swan River and intermittently open Moore River estuaries on the lower west coast of Australia (31–32°S) and from the permanently open Nornalup Walpole and normally closed Wellstead estuaries (34–35°S) on the southern coast of Western Australia (see Fig. 1 for locations of these estuaries). *Acanthopagrus butcheri* was also collected from Lake Clifton, a landlocked saline, coastal lake. Because the Department of Conservation and Land Management (CALM) restricted the number of *A. butcheri* that could be collected from this lake to 100, and because 85 of these 100 fish were males, emphasis was placed on the data obtained for this sex in this lacustrine environment.

Fish in estuaries were collected from over sand in nearshore, shallow waters (<1.5 m depth) by using a 41-m seine net with 9-mm mesh in the codend and from offshore, deeper waters (2–5 m depth) by employing composite sunken gill nets containing eight 20 m long × 2 m high panels, each of which had a different mesh size, i.e. 38, 51, 63, 76, 89, 102, 115, or 127 mm. Sampling in the Swan River Estuary commenced in September 1993 and was carried out monthly until April 1995 with seine netting and monthly until February 1995 with gill netting. The same methods were used to sample *A. butcheri* in the Moore River, Nornalup Walpole, and Wellstead estuaries between the spring of 1993 and the summer of 1996–97 (December–January). Sampling in the Swan River, Nornalup Walpole, and Wellstead estuaries was carried out in the saline lower reaches of the tributary rivers, i.e. upper estuary (Fig. 1), which, for most of the year, contain the majority of the *A. butcheri* found in those estuaries (Sarre and Potter, 1999). In contrast, sampling was undertaken throughout the short Moore River Estuary, which does not possess the large central basins that are found in the other three estuaries (Fig. 1). The catches obtained by seine and gill netting in the above four estuaries were supplemented by up to a further 7% by fish obtained with rod and line. A fine mesh seine net, which was 5.5 m long and consisted of 1-mm mesh, was used to collect small *A. butcheri* from extensive beds of the macroalgae *Gracilaria verrucosa* in the downstream and middle regions of the upper Swan River Estuary between December 1998 and March 1999. (See "Results" section for the reason for this additional sampling). The sample of 100 *A. butcheri* collected from Lake Clifton in November 1996 was obtained exclusively by rod and line, in accordance with the conditions laid down by CALM.

Both of the sagittal otoliths were removed from each fish sampled from the four estuaries and Lake Clifton and these otoliths were immersed in methyl salicylate solution. For sectioning, otoliths were mounted and embedded in clear epoxy resin and cut into ca 0.5-mm transverse sections with an Isomet low-speed diamond saw. Sections were ground on sequentially finer grades of carborundum paper (400–1200 grade) and mounted on glass slides with DePX mounting adhesive. Whole otoliths and sectioned otoliths were placed on a black surface and examined microscopically under reflected light.

Measurements were made of the distance between the outer edge of the outermost opaque zone and the periphery of the otolith in the case of the otoliths that were to be used for aging fish in the Swan River Estuary. This distance, i.e. the marginal increment, was then expressed either as a proportion of the distance between the primordium of the otolith and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edge of the two outermost opaque zones, when two or more opaque zones were present. All measurements were recorded to the nearest 0.05 mm. As with other sparids, a narrow opaque zone is laid down in the otoliths of *A. butcheri* during the cool (winter) period and a wide translucent zone is deposited during the warm (summer) period (Johnson, 1983; Buxton and Clarke, 1991; Francis et al*.,* 1992; Booth and Buxton, 1997).

Otoliths from 239 *A. butcheri*, collected from the Swan River Estuary and covering a wide size range, were used for comparing the number of narrow, opaque zones that could be seen on this hard structure before and after sectioning. The number of opaque zones visible in a subsam-
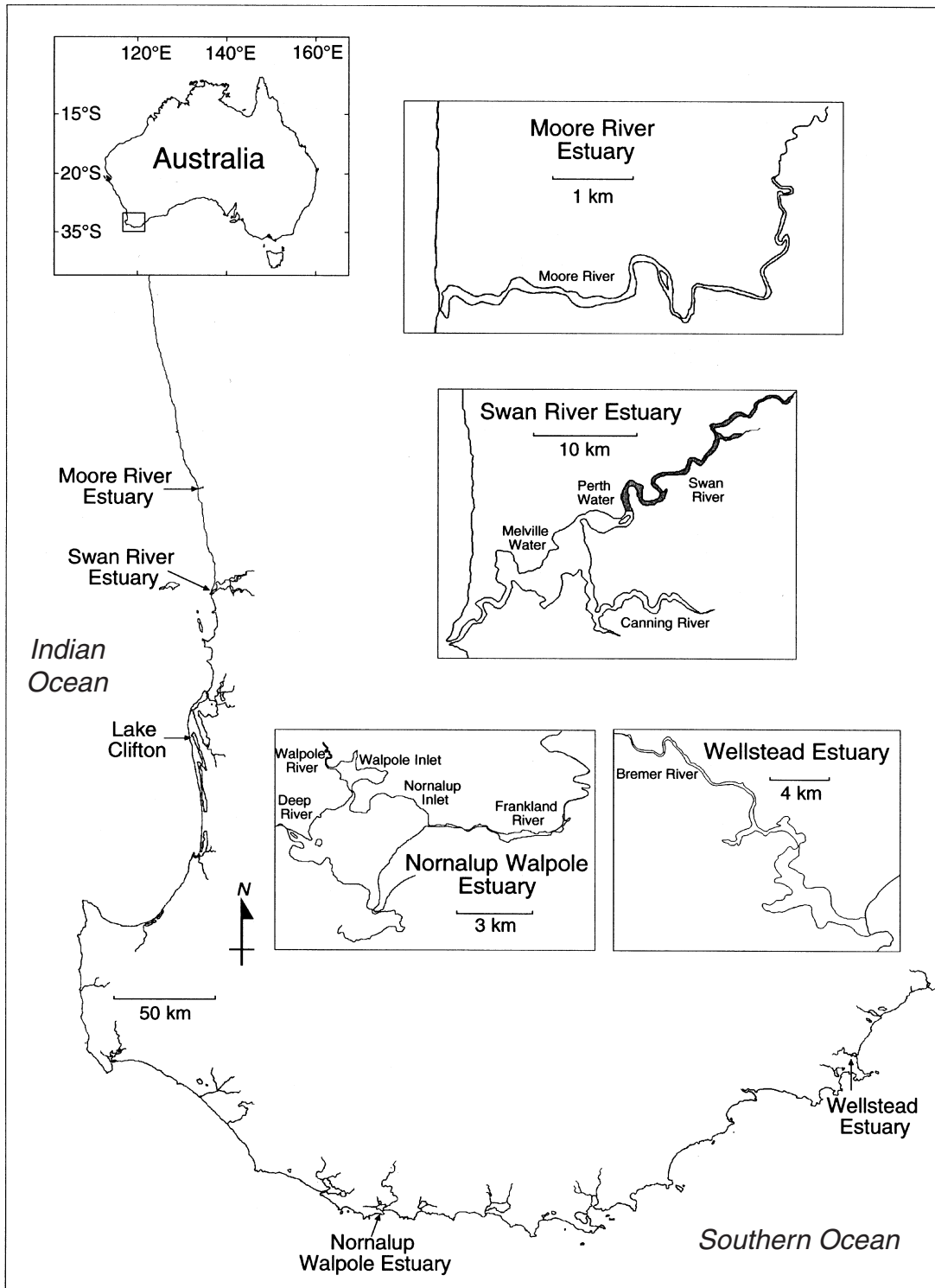
Figure 1

Map showing the location of the four estuaries and Lake Clifton in southwestern Australia from which samples of *Acanthopagrus butcheri* were collected, together with individual maps of each estuary. The shaded area of the Swan River Estuary represents the region sampled in our study.

ple of 126 of the sectioned otoliths were then compared with the numbers of annuli on scales removed from the same fish. The scales used for these comparisons, which were obtained from above the lateral line and directly behind the operculum, were mounted between glass slides and examined microscopically under reflected light.

The number of opaque zones in the whole and sectioned otoliths of a subsample of 162 of the above 239 fish and the number of annuli on the scales of a random subsample of 87 of those fish were also counted by a second reader to determine the level of reproducibility of the counts made of the growth zones on these hard structures by the senior author.

The birth date assigned to *A. butcheri* in each water body corresponds to peak spawning activity, as estimated from the trends exhibited by gonadosomatic indices, stages in gonadal development and pattern of oocyte development (Sarre and Potter, 1999). Von Bertalanffy growth curves were fitted to the individual lengths of female and male fish at their estimated ages at capture by a nonlinear technique (Gallucci and Quinn, 1979) by using a nonlinear subroutine in SPSS (SPSS Inc., 1988). The von Bertalanffy equation is

$$L_t = L_\infty \left[1 - e^{-k(t - t_0)} \right],$$

where L_t = the total length at age t (years);
　　　　L_∞ = the mean of the asymptote predicted by the equation;
　　　　k = the growth coefficient; and
　　　　t_0 = the hypothetical age at which fish would have zero length, if growth followed that predicted by the equation.

The lengths at age of fish whose sex could not be determined under a dissecting microscope were selected at random and placed alternately in the data sets for female and male fish.

Each of the growth parameter estimates for female and male fish in the same estuary and for each sex in the four estuaries were compared by using a likelihood ratio test (see Kimura, 1980). Comparisons were also made between the growth parameters for the males of *A. butcheri* in Lake Clifton, the sex which dominated the catches in that lake, and those of the males of this species in the four estuaries.

The likelihood ratio for the null hypothesis (Kimura, 1980) tests the null hypothesis against the alternative hypothesis where

H_w states that the parameters L_∞, k, and t_0 satisfy some set of r linear constraints;

H_Ω states that the parameters L_∞, k, and t_0 possibly satisfy no linear constraints.

The maximum likelihood estimates of the error variances $\hat{\sigma}_w^2$ and $\hat{\sigma}_\Omega^2(r)$ are given by the sum of squares of residuals from the iteratively reweighted least squares procedure used to fit L_∞, k, and t_0 subject to r linear constraints.

The likelihood ratio test statistic, as described by Cerrato (1990), for two data sets with sample sizes n_1 and n_2 is given by

$$-2\log(\Lambda),$$

where　　　　$\Lambda = \left(\dfrac{\hat{\sigma}_{1\omega}^2}{\hat{\sigma}_{1\Omega}^2} \right)^{-n_1/2} \left(\dfrac{\hat{\sigma}_{2\omega}^2}{\hat{\sigma}_{2\Omega}^2} \right)^{-n_2/2}.$

Table 1

The linear constraints and degrees of freedom of each hypothesis, based on Kimura (1980), where $_M$ and $_F$ represent males and females, respectively.

Hypothesis	Linear constraints	Degrees of freedom
H_Ω	none	
$H_{\omega 1}$	$L_{\infty M} = L_{\infty F}$	1
$H_{\omega 2}$	$k_M = k_F$	1
$H_{\omega \beta}$	$t_{0M} = t_{0F}$	1

Under the null hypothesis $-2\log(\Lambda)$ converges to a $\chi^2(r)$ distribution with the degrees of freedom equal to the number of equations required to specify the linear constraints applied to the model (Kimura, 1980). The null hypothesis is rejected at the α level of significance when $-2\log(\Lambda) > \chi^2(r)$.

The types of linear constraints applied to the von Bertalanffy growth equation, the null and alternative hypotheses associated with each constraint and the degrees of freedom of the test statistic are given in Table 1.

Results

Validation of annual deposition of opaque zones in otoliths

The mean monthly marginal increment on sectioned otoliths with one opaque zone declined sharply from 0.57 in September and October 1993 to 0.11 in November 1993, before gradually rising to a maximum of 0.93 in October 1994 (Fig. 2). As in 1993, the mean marginal increment then declined markedly between October and November 1994 and subsequently rose over the ensuing months. The trends exhibited by the mean monthly marginal increment on otoliths with two and three opaque zones were the same as those just described for otoliths with one opaque zone (Fig. 2). Because the number of fish with otoliths displaying four or more opaque zones in the samples for some months was small, the marginal increments for all such otoliths in each month were pooled. Although the trends shown by the mean monthly marginal increments on these otoliths were not quite as "smooth" as those shown by otoliths with one to three opaque zones, they still clearly declined precipitously in November of both 1993 and 1994 and subsequently rose progressively during the ensuing months between early summer and mid-autumn (Fig. 2).

The fact that, irrespective of the number of opaque zones on otoliths, the mean monthly marginal increments on otoliths underwent a pronounced decline and then a progressive rise only once during the year demonstrates that a single opaque zone is formed in otoliths each year. Thus, the number of opaque zones in sectioned otoliths can be used to determine the age of *A. butcheri*.
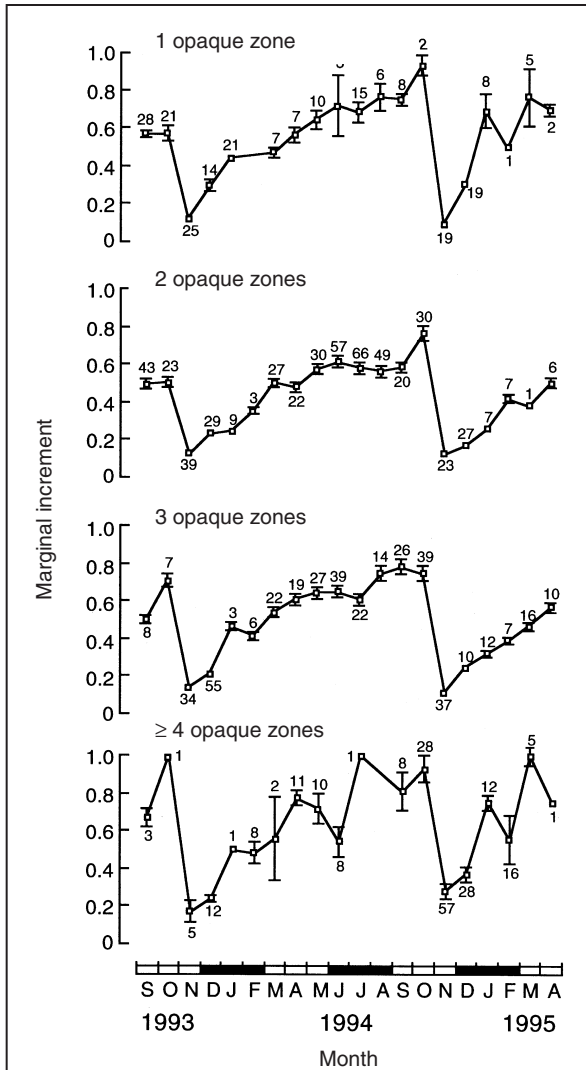
Figure 2

Mean monthly marginal increments ±1SE for sectioned sagittal otoliths of *Acanthopagrus butcheri* in the upper Swan River Estuary. The mean marginal increment is expressed as a proportion of the distance between the primordium and the edge of the opaque zone, when only one such zone was present, and as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more such zones were present. Sample sizes are given for each month.
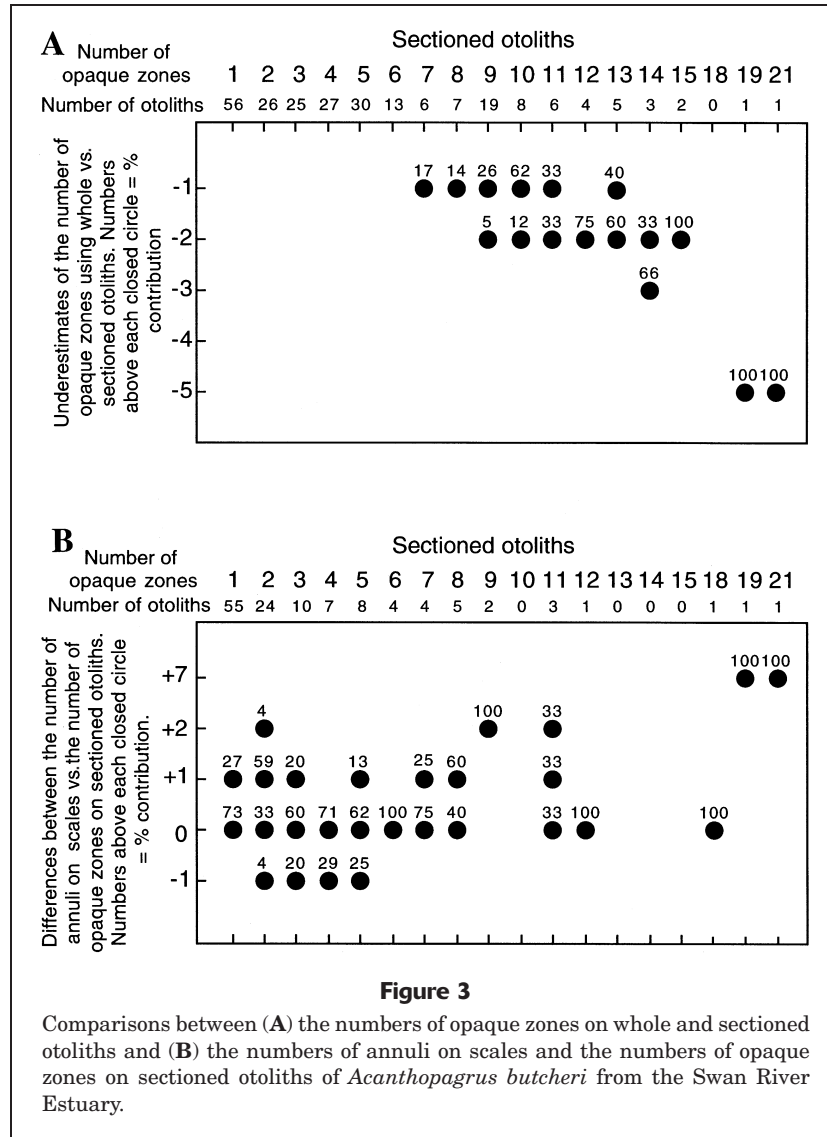
underestimated the age of two 14-year-old fish by three years, two 15-year-old fish by two years, and one 19- and one 21-year-old fish by five years each (Fig. 3A).

The numbers of annuli observed on the scales of *A. butcheri* differed from those recorded in 27, 67, and 40% of the sectioned sagittal otoliths of the same fish, when the otoliths possessed one, two, and three opaque zones, respectively (Fig. 3B). The number of annuli exceeded that of the number of opaque zones in 34% of all cases. The number of annuli on the scales of fish, in which the sectioned otoliths possessed eight to eleven opaque zones, exceeded by one or two the number of opaque zones on those otoliths in 70% of cases (Fig. 3B). On the basis of the number of opaque zones on their sectioned otoliths, one fish that was estimated as 19 and another as 21 years old, displayed seven more annuli on their scales than on their otoliths. Although the number of sectioned otoliths with more than six opaque zones, that were used for comparisons with scales, was only 18, it is still noteworthy that the number of opaque zones on more than half of those otoliths was less than the number of circuli on the scales obtained from the corresponding fish.

The number of opaque zones recorded independently by a second "reader" for sectioned otoliths of *A. butcheri* with 0–3 zones (50 fish), 4–6 zones (50 fish) and 7–10 zones (40 fish), were always the same as those recorded by the senior author for the same otoliths. Furthermore, the second reader recorded the same number of opaque zones on all but two of the 22 sectioned otoliths that the senior author had recorded as having 11 or more opaque zones. Moreover, after reviewing and discussing the two discrepancies, the second reader agreed that he had failed to detect one of the least conspicuous opaque zones near the periphery of the two otoliths for which there were discrepancies, and therefore his counts agreed with the counts made by the senior author. However, the number of annuli counted on the scales by the second reader, that had previously been recorded by the senior author as having 0–3 annuli (50 fish), 4–10 annuli (30 fish), and ≥11 annuli (7 fish), differed in 20%, 43%, and 86% of cases, respectively, which reflects the difficulty in detecting annuli on scales. The differences between counts ranged from one on scales with 0–3 annuli to more than five on scales with ≥11 annuli.

Trends exhibited by length-frequency data for different age classes

The data presented earlier demonstrated that the number of opaque zones on whole otoliths of *A. butcheri* could be used for aging this sparid when there were six or less opaque zones present (Fig. 3A). However, the data in Fig. 3A showed that otoliths had to be sectioned to consistently reveal all of their opaque zones when they displayed seven or more such zones prior to sectioning. Thus, to reduce the margin for producing invalid counts to a minimum, estimates of the age of individual *A. butcheri* were made by using whole otoliths, when five or less opaque zones were present, and by employing sectioned otoliths, when six or more such zones were present.

Number of growth zones on hard structures

The number of opaque zones detected on a sectioned otolith of *A. butcheri* was always the same as the number observed on the same otolith prior to sectioning, when six or less such zones were visible on the whole otolith (Fig. 3A). However, the use of whole otoliths would have underestimated by one year 15% of seven- and eight-year-old fish, collectively, and, by one or two years, 57% of nine- to 13-year-old fish, collectively. The use of whole otoliths would also have

A Number of opaque zones

Sectioned otoliths

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19	21
Number of otoliths	56	26	25	27	30	13	6	7	19	8	6	4	5	3	2	0	1	1

B Number of opaque zones

Sectioned otoliths

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	19	21
Number of otoliths	55	24	10	7	8	4	4	5	2	0	3	1	0	0	0	1	1	1

Figure 3

Comparisons between (**A**) the numbers of opaque zones on whole and sectioned otoliths and (**B**) the numbers of annuli on scales and the numbers of opaque zones on sectioned otoliths of *Acanthopagrus butcheri* from the Swan River Estuary.

Although seine netting over sand in nearshore, shallow waters of the upper Swan River Estuary in the summer and early autumn of both 1993–94 and 1994–95 yielded many *A. butcheri* of 50 to 180 mm, it produced only a few smaller individuals of this species. However, sampling of beds of the macroalgae *Gracilaria verrucosa* in the same period in 1998–99 yielded considerable numbers of *A. butcheri* that ranged in length from 16 to 60 mm. Once *A. butcheri* reached lengths of ca. 60 mm, they moved from the beds of *G. verrucosa* to reside over sand. The lengths of these *A. butcheri*, which represented the 0+ recruits resulting from spawning from November to December of 1998 (Sarre and Potter, 1999), and thus represented the 1998 year class, increased from 16–32 mm in December 1998 to 26–63 mm in January 1999 to 44–86 mm in February 1999 and to 36–112 mm in March 1999 (Fig. 4). The mean length ±1SE in the latter month, i.e. 76 mm, did not differ significantly (*P*>0.05) from that of the 0+ age class in March 1994, when a substantial number of these small fish were also caught (Fig. 5).

Because *A. butcheri* spawns predominantly between October and January (spawning peaking in November [Sarre and Potter, 1999]), the cohort of small *A. butcheri* (81–115 mm), that was caught by seine net in the shallow waters of the Swan Estuary in September 1993 and whose otoliths did not possess an opaque zone, was the product of the spawning that took place in the spring to early summer of the previous year, i.e. 1992 (Fig. 5). The lengths of this 1992 year class increased from 81–115 mm in September 1993 to 100–152 mm in November 1993, by which time a single and narrow opaque zone could be discerned on the edge of the otoliths of this year class. Because spawning peaks in November, the members of this cohort were thus now about one year old. By November and December 1994, the lengths of this 1992 year class, now representing early 2+ fish, had increased to 170–220 and 189–224 mm, respectively. The 1993 year class first appeared in seine net catches in March 1994 at lengths of 67–102 mm and was caught until May, when its

Figure 4

Length-frequency histograms for juvenile *Acanthopagrus butcheri* caught with a 5.5-m seine net (1-mm mesh) in the shallows (<1 m) of the upper Swan River Estuary between December 1998 and March 1999. Numbers in parentheses represent the number of fish measured.

Maximum size and age and von Bertalanffy growth parameters

The spawning activity of *A. butcheri* peaked in early November in the Swan River, Moore River, and Nornalup Walpole estuaries and in early October in the Wellstead Estuary (Sarre and Potter, 1999). The von Bertalanffy growth curves for *A. butcheri* were thus derived by using a birth date of 1 November for the first three estuaries and 1 October for the Wellstead Estuary. Because many fully mature fish were found in Lake Clifton in early November, and this lake was located near the Swan River Estuary, a birth date of 1 November was likewise assigned to the population of *A. butcheri* in that system.

The lowest maximum lengths of female and male *A. butcheri* were 377 and 365 mm, respectively, which were recorded for fish caught in the Wellstead Estuary, whereas the greatest maximum lengths of each sex was 480 mm recorded for a female in the Swan River Estuary and 485 mm recorded for a male in Lake Clifton (Table 2). The maximum weights of *A. butcheri* in the five systems ranged from a low of 862 g for a female in the Wellstead Estuary to 2196 g for a female in the Swan River Estuary (Table 2). The maximum age of both sexes in each estuary was at least 15 years and the maximum age attained in any system was the 21 years recorded for both a female in the Swan River Estuary and a male in the Nornalup Walpole Estuary (Table 2).

The growth curves of male *A. butcheri* in the Swan River, Nornalup Walpole, and Wellstead estuaries and Lake Clifton followed similar overall trends and thus never crossed one another, and the same was true for the growth curves for females in the above three estuaries (Figs. 6 and 7). The rates of increase in the lengths of both sexes in the Moore River Estuary were initially slower than in each of the above three estuaries, and the rate of increase in the length of males in the Moore River Estuary was also initially less than that of this sex in Lake Clifton. (Note that there were insufficient data for the females in Lake Clifton to make similar comparisons with this sex in this system.) The far slower rate at which length initially increased in the Moore River Estuary is illustrated by the fact that, when male fish were 35–37 months old, i.e. three years in age, their mean length in this estuary was only 151 mm and significantly lower ($P<0.001$) than the 272 mm in the Swan River Estuary, 162 mm in the Nornalup Walpole Estuary, 204 mm in the Wellstead Estuary, and 339 mm in Lake Clifton. Likewise, the mean length of females of *A. butcheri* in the Moore River Estuary at this age was only 144 mm and thus significantly lower than the 285, 161, and 212 mm recorded in the Swan, Nornalup Walpole, and Wellstead estuaries, respectively. It is also noteworthy that the above-mean lengths of males in each of the five systems were significantly different from each other in all cases, except for *A. butcheri* from the Nornalup Walpole and Wellstead estuaries. Corresponding results were obtained for females in the four estuaries. As *A. butcheri* in the Moore River Estuary reached an older age, the growth curves for males and females in this estuary then crossed those for fish from the Nornalup Walpole and Well-

lengths had reached 104–139 mm. When representatives of the 1993 year class reappeared in catches in September 1994, their lengths were still only 96–135 mm, indicating that growth had not occurred during the immediately preceding winter months. The lengths of the 1993 year class subsequently increased to between 136 and 183 mm in January 1995 (Fig. 5). Although the 1994 year class first appeared in March 1995, i.e. in the corresponding month to when the 1993 year class appeared in the previous year, its numbers were small and it was not represented in the following month, i.e. April (Fig. 5).

The 1991 year class was well represented in the majority of months (Fig. 5). The lengths of this strong cohort increased from 163–235 mm in September 1993 to 220–296 mm in September 1994 and to 222–325 mm in November 1994, at which time the fish were entering their fourth year of life. The 1990 year class was a particularly strong cohort (Fig. 5). The lengths of this year class increased from 208–304 mm in September 1993 to 268–349 mm in September 1994 and 259–360 mm at the commencement of their fifth year of life in November. The numbers of fish belonging to earlier year classes, i.e. the 1989, 1988, 1987 year classes, etc., were very low (Fig. 5). Thus, the number of older fish collectively in the Swan River Estuary was also low.
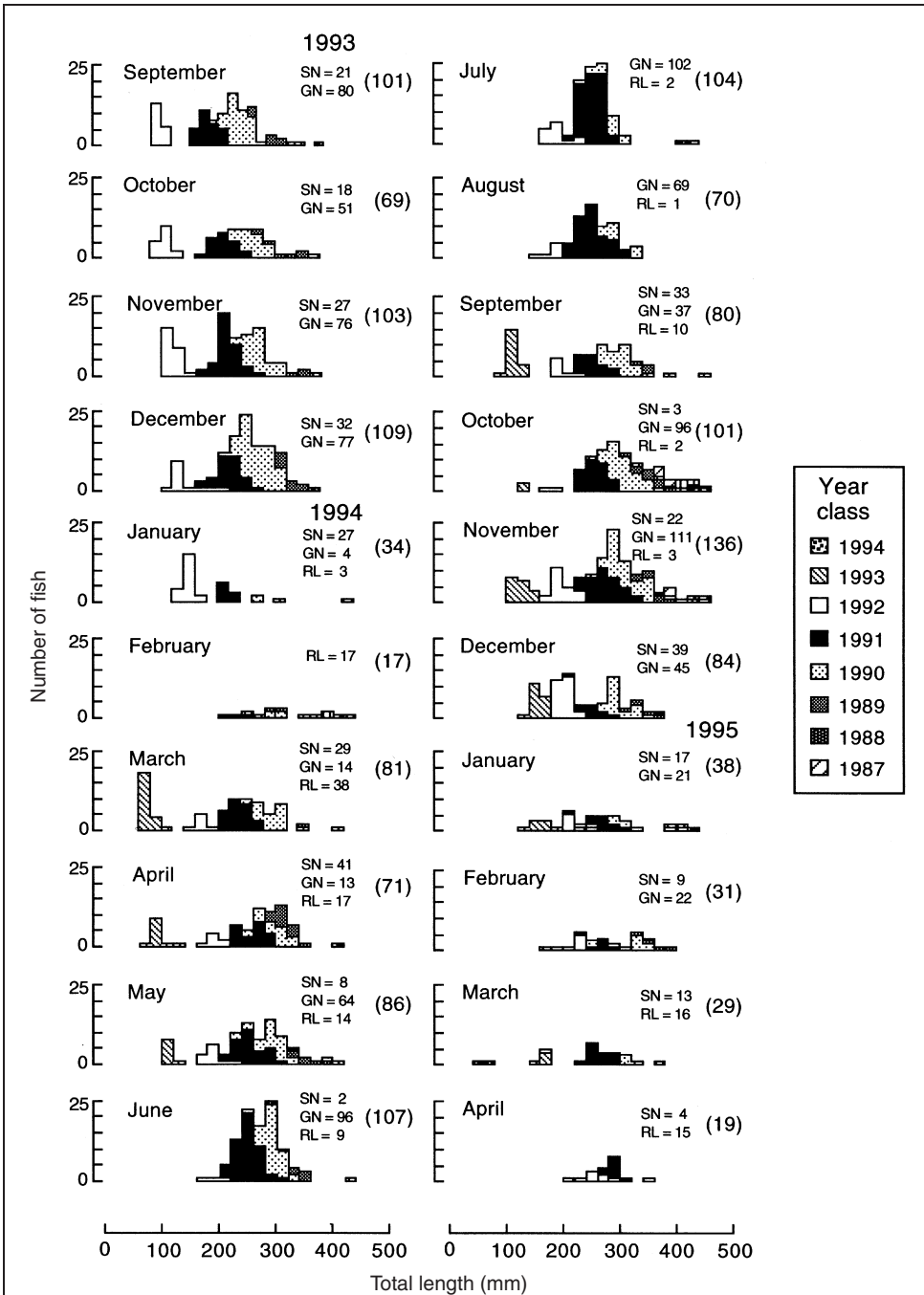
Figure 5

Length-frequency histograms for the different year classes of *Acanthopagrus butcheri,* with data derived from samples of males and females collectively that were caught with seine and gill nets in the upper Swan River Estuary between September 1993 and April 1995. Sample sizes in each month are given for seine netting (SN), gill netting (GN) and rod and line (RL) and in parenthesis for the total sample.

stead estuaries. This feature was reflected in significantly greater asymptotic lengths and lower k values for the Moore River Estuary population than those derived for fish in the latter two estuaries (Table 2, Figs. 6 and 7).

The likelihood ratio test demonstrated that neither the ages at length zero (t_0) nor the growth coefficients (k) in the von Bertalanffy growth equations differed significantly between female and male *A. butcheri* in either the
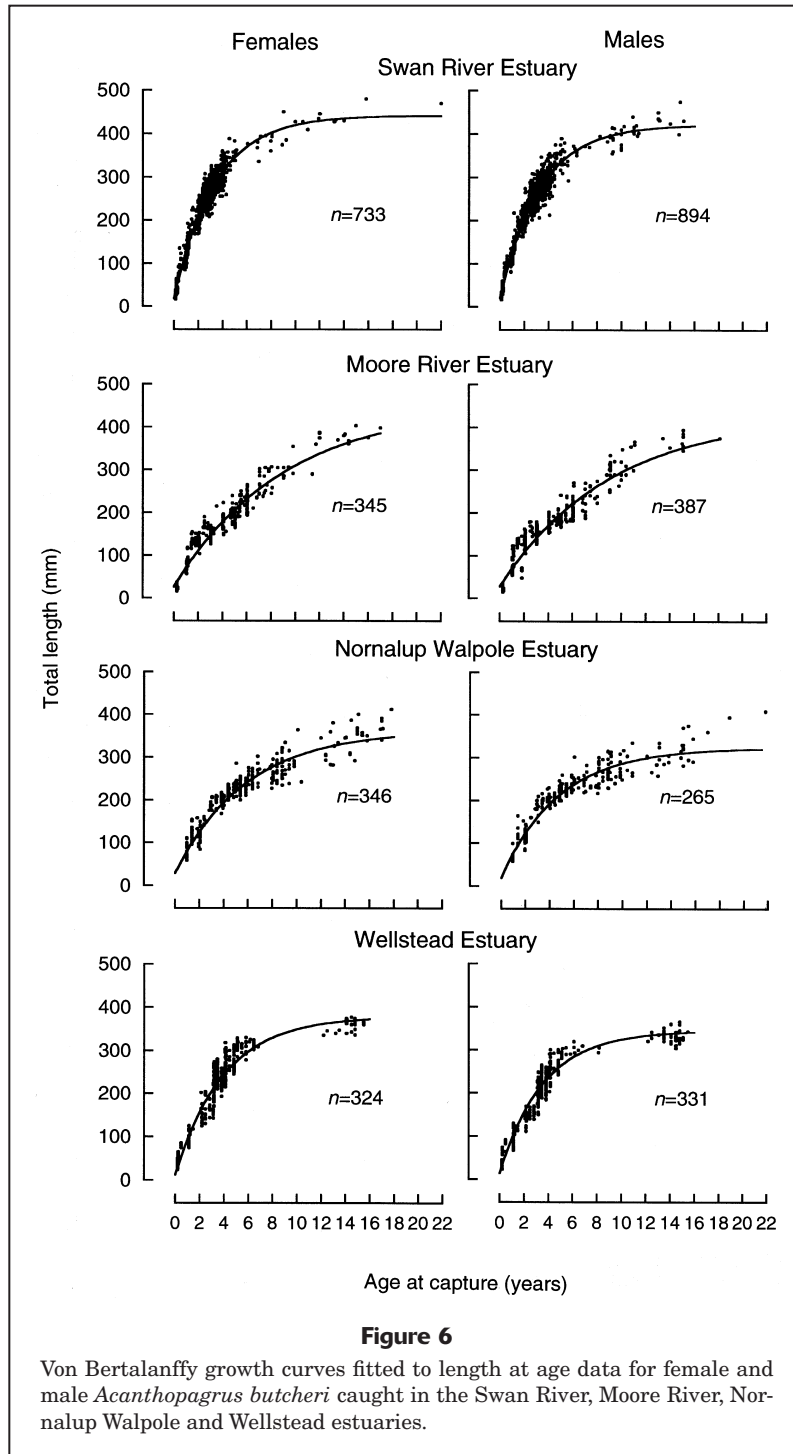
Table 2

Von Bertalanffy growth parameters and confidence intervals (95%) derived from length-at-age data for female and male *Acanthopagrus butcheri* caught in the Swan River, Moore River, Nornalup Walpole and Wellstead estuaries and for the males in Lake Clifton. n is sample size and L_{max}, W_{max}, and A_{max} are the maximum lengths (mm), weights (g), and ages, respectively. t_0 is the hypothetical age at which fish would have zero length, k is the growth coefficient, L_∞ is the asymptotic length and r^2 is the coefficient of determination.

	n	L_{max}	W_{max}	A_{max}	t_0	k	L_∞	r^2

	n	L_{max}	W_{max}	A_{max}	t_0	k	L_∞	r^2
Swan River								
Females	733	480	2196	21	−0.13	0.30	437.8	0.94
95% CL (lower)					−0.17	0.28	426.0	
95% CL (upper)					−0.10	0.31	449.5	
Males	894	475	1780	15	−0.15	0.31	419.3	0.94
95% CL (lower)					−0.19	0.29	10.7	
95% CL (upper)					−0.11	0.32	427.9	
Moore River								
Females	345	403	1192	17	−0.54	0.11	451.6	0.93
95% CL (lower)					−0.68	0.09	416.3	
95% CL (upper)					−0.41	0.12	486.9	
Males	387	394	1162	18	−0.61	0.11	429.2	0.92
95% CL (lower)					−0.76	0.09	395.9	
95% CL (upper)					−0.46	0.12	462.6	
Nornalup Walpole								
Females	346	412	1250	17	−0.60	0.16	367.0	0.91
95% CL (lower)					−0.88	0.14	352.5	
95% CL (upper)					−0.43	0.18	381.6	
Males	265	409	1148	21	−0.31	0.21	323.0	0.90
95% CL (lower)					−0.54	0.19	311.8	
95% CL (upper)					−0.08	0.24	334.6	
Wellstead								
Females	324	377	862	15	−0.17	0.25	377.8	0.91
95% CL (lower)					−0.27	0.23	365.3	
95% CL (upper)					−0.07	0.27	390.3	
Males	331	365	1247	15	−0.18	0.27	344.6	0.92
95% CL (lower)					−0.28	0.25	335.8	
95% CL (upper)					−0.08	0.29	353.4	
Lake Clifton								
Males	85	485	1914	18	−0.46	0.32	441.5	0.96
95% CL (lower)					−0.66	0.28	453.4	
95% CL (upper)					−0.26	0.36	429.6	

Swan River, Moore River or Wellstead estuaries (Table 3). Furthermore, although these two growth parameters did differ significantly between the two sexes in the Nornalup Walpole Estuary, the probability levels in both cases were close to 0.05. However, the asymptotic length (L_∞) for female fish was significantly greater than that of male fish in each estuary except that of the Moore River (Table 3).

The values for k and L_∞ for each sex differed significantly among the populations of *A. butcheri* in the four estuaries and between those of males in each of these estuaries and Lake Clifton ($P<0.001$ or 0.01). Furthermore, the values for t_0 for each sex almost invariably differed significantly ($P<0.001$ or <0.05) among the populations in the four estuaries and between those of males in each of these estuaries and Lake Clifton. Because the three von Bertalanffy parameters for both sexes were each shown almost invariably to differ significantly among the different populations, no attempt was made to test whether there was a common pattern of growth for each sex in each system.

Figure 6

Von Bertalanffy growth curves fitted to length at age data for female and male *Acanthopagrus butcheri* caught in the Swan River, Moore River, Nornalup Walpole and Wellstead estuaries.

The values for k for *A. butcheri* were least in the Moore River Estuary, i.e. 0.11, and greatest in Lake Clifton, i.e. 0.32 (Table 2). The values for L_∞ ranged from a low of 367.0 mm for females and 323.0 mm for males in the Nornalup Walpole Estuary to a high of 451.6 and 441.5 mm for the corresponding sexes in the Moore River Estuary and Lake Clifton, respectively (Table 2). Estimates of t_0 for both sexes of *A. butcheri* in the four estuaries and of the

males of *A. butcheri* in Lake Clifton all lay within the relatively narrow range of –0.13 to –0.61 years (Table 2).

Length–weight relationships

The equations relating total length and weight of female and male *A. butcheri* in each estuary and for males in Lake Clifton are presented below, so that, when required, the approxi-

mate weights of fish of a particular length can be estimated. Becasue analysis of covariance (ANCOVA) showed that neither the slopes nor the *y*-intercepts in the equations for

female and male fish in each estuary differed significantly ($P > 0.05$), the equations relating total length and weight for both sexes combined in each estuary are also presented.

Swan River Estuary
    Females: $\log_{10} W = -5.09 + 3.14 \log_{10} L$ ($r^2 = 0.99$, $n = 865$).
    Males: $\log_{10} W = -5.10 + 3.14 \log_{10} L$ ($r^2 = 0.99$, $n = 925$).
    Pooled: $\log_{10} W = -5.07 + 3.14 \log_{10} L$ ($r^2 = 0.99$, $n = 1790$).

Moore River Estuary
    Females: $\log_{10} W = -5.10 + 3.13 \log_{10} L$ ($r^2 = 0.99$, $n = 250$).
    Males: $\log_{10} W = -5.14 + 3.15 \log_{10} L$ ($r^2 = 0.99$, $n = 287$).
    Pooled: $\log_{10} W = -5.12 + 3.13 \log_{10} L$ ($r^2 = 0.99$, $n = 537$).

Nornalup Walpole Estuary
    Females: $\log_{10} W = -4.99 + 3.07 \log_{10} L$ ($r^2 = 0.99$, $n = 302$).
    Males: $\log_{10} W = -5.03 + 3.09 \log_{10} L$ ($r^2 = 0.99$, $n = 234$).
    Pooled: $\log_{10} W = -5.00 + 3.08 \log_{10} L$ ($r^2 = 0.99$, $n = 536$).

Wellstead Estuary
    Females: $\log_{10} W = -4.84 + 3.01 \log_{10} L$ ($r^2 = 0.99$, $n = 274$).
    Males: $\log_{10} W = -4.89 + 3.03 \log_{10} L$ ($r^2 = 0.99$, $n = 278$).
    Pooled: $\log_{10} W = -4.85 + 3.02 \log_{10} L$ ($r^2 = 0.99$, $n = 552$).

Lake Clifton
    Males: $\log_{10} W = -5.12 + 3.14 \log_{10} L$ ($r^2 = 0.98$, $n = 85$).
    Pooled: $\log_{10} W = -5.10 + 3.13 \log_{10} L$ ($r^2 = 0.99$, $n = 100$).

Discussion

Validation of the method for aging *Acanthopagrus butcheri*

Our study shows that a growth zone is not laid down in the otoliths of the 0+ age class of *Acanthopagrus butcheri* until winter and that this growth zone does not become clearly delineated until late spring. Because spawning peaks in early November in the Swan Estuary (Sarre and Potter, 1999), the first growth zone becomes delineated as the individuals of this species become one year old. Furthermore, the trends exhibited by the marginal increments on the sectioned otoliths of *A. butcheri* demonstrate that an opaque zone is laid down annually in this hard structure. Our results also demonstrate that the otoliths of *A. butcheri* do not need to be sectioned in order to consistently reveal all of the opaque zones until they had reached a size at which they possessed seven or more such zones. Validation that the opaque zones, which are revealed on the otoliths of *A. butcheri* by sectioning, are formed annually, implies that the estimates of the ages of individual black bream recorded by Morison et al. (1998) using sectioned otoliths are valid for fish caught in the Gippsland Lakes in eastern Australia. However, because the number of annuli on scales frequently differed from the number of opaque zones on sectioned otoliths from the same fish, the number of annuli on scales do not provide a reliable method for aging *A. butcheri*. Thus, those estimates of the age of individual *A. butcheri*, that have been based on the number

Table 3

Significance levels for comparisons between the von Bertalanffy growth parameters for female and male *Acanthopagrus butcheri* caught in each of the Swan River, Moore River, Nornalup Walpole, and Wellstead estuaries by using the likelihood ratio test. ***=$P<0.001$, **=$P<0.01$, *=$P<0.05$, NS = Not significant. t_0 is the hypothetical age at which fish would have zero length, k is the growth coefficient, and L_∞ is the asymptotic length.

Estuary	von Bertalanffy growth parameter		
	t_0	k	L_∞
Swan	NS	NS	**
Moore	NS	NS	NS
Nornalup Walpole	*	*	***
Wellstead	NS	NS	***

of annuli on scales (Butcher, 1945; Thomson, 1957; Weng, 1971; Hobday and Moran[3]) are, in many cases, probably invalid.

Differences in age structures amongst populations

Because the majority of *A. butcheri* obtained from the Swan River, Moore River, Nornalup Walpole, and Wellstead estuaries were collected by using the same seine and

gill net sampling regimes, supplemented with a limited amount of angling, any gross differences in the age structure of samples from populations in the different estuaries almost certainly represent real differences. The percentage of *A. butcheri* caught at ≥5 years of age in the Swan River Estuary (5%) was far lower than in either the Moore River Estuary (30%), approximately 100 km farther north on the lower west coast of Australia, or the Nornalup Walpole Estuary (45%) on the south coast of Australia. Note that the estimate for the Swan River Estuary was restricted to data collected during the main sampling period and did not thus include the large samples of small fish that were caught between December 1998 and March 1999. The above differences in the proportion of older fish presumably reflect a greater "mortality" of older fish in the Swan River Estuary than in the other estuaries. It thus

appears highly relevant that the population of *A. butcheri* in the Swan River Estuary is exposed to heavy fishing pressure from the recreational sector throughout the year and from commercial fishermen during winter and early spring, whereas the population in the Moore River Estuary is lightly fished and that in the Nornalup Walpole Estuary is not exposed to commercial fishing (Sarre and Potter, 1999).

Although representatives of all age classes up to 15+ were recorded for the populations of *A. butcheri* in each of the above three estuaries, this was not the case with the Wellstead Estuary, which is located 300 km to the east of the Nornalup Walpole Estuary. Thus, in the samples collected from this estuary in 1995 and 1996, the 1989, 1987, 1986, 1985, and 1984 year classes were not represented, and the 1988 year class was represented by only two fish (Fig. 6). This strong implication that, in the Wellstead Estuary, *A. butcheri* either does not spawn or has very limited spawning success in some years parallels the situation recorded for this species in the Gippsland Lakes in eastern Australia (Morison et al., 1998; Hobday and Moran[3]; Coutin et al.[4]). The work of Morison et al. (1998) demonstrated that, in that latter estuary, the commercial catches of *A. butcheri* between 1993 and 1996 were dominated by two year classes and that there had been no strong recruitment of *A. butcheri* since 1989. The absence or weakness of certain year classes in the Gippsland Lakes, and also in the Hopkins River Estuary which is also in eastern Australia, has been attributed to the detrimental influence on spawning success of such unfavourable environmental conditions as heavy freshwater discharge or unsuitable salinities (Newton, 1996; Hobday and Moran[3]). Thus, in the context of the absence of the 1984 year class in samples, it appears relevant that, in the Wellstead Estuary, which has normally remained closed during the last 30 years, there was, as a result of "cyclonic rainfall," an extremely protracted period of heavy freshwater discharge between the early spring of 1984 and the autumn of 1985 (Hodgkin and Clark[5]). This led to a very severe scouring of the substrate and a breaching of the bar at the mouth of this estuary, with the result that this mouth remained open between September 1984 and May 1985. The heavy freshwater discharge that occurred during and immediately after the 1985 spawning season of *A. butcheri* in the Wellstead Estuary would thus almost cer-
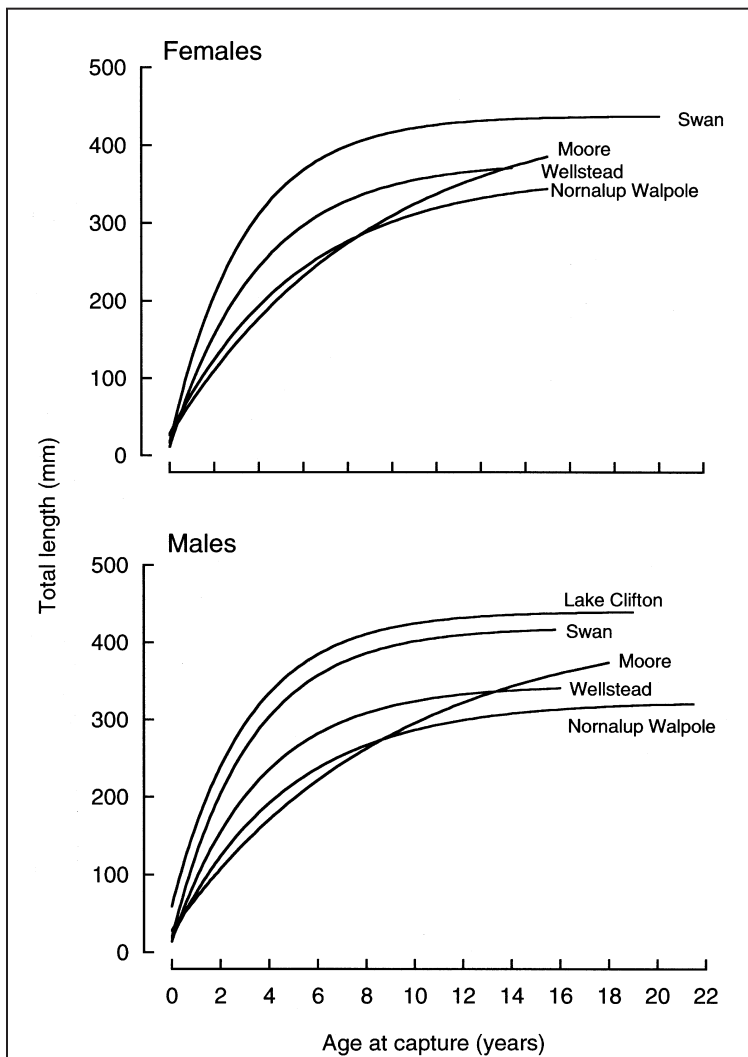

Figure 7

Comparisons between von Bertalanffy growth curves fitted to length-at-age data for female and male *Acanthopagrus butcheri* in the Swan River, Moore River, Nornalup Walpole, and Wellstead estuaries and for males in Lake Clifton in southwestern Australia.

[4] Coutin, P., S. Walker, and A. Morison. 1997. Black bream—1996. Compiled by the Bay & Inlet Fisheries and Stock Assessment Group. Fisheries Victoria Assessment Report 14. Melbourne, Victoria, Australia, 89 p.

[5] Hodgkin, E. P., and R. Clark. 1987. Wellstead Estuary, the estuary of the Bremer River. Estuarine Study Series 1. Environmental Protection Authority, Perth, Western Australia, 22 p.

tainly have flushed out to sea any eggs or larvae of this species that were produced during that period. However, it should also be recognized that freshwater discharge was so strong during that period that even many large *A. butcheri* were flushed out of the estuary, with the result that some of these fish were subsequently caught by anglers along the nearby coast (Spurr[6]). Furthermore, when freshwater discharge is very high, the salinities fall to such low levels that they are unlikely to be conducive to spawning by *A. butcheri* (Haddy and Pankhurst, 2000). Thus, the absence of the 1984 year class in samples may be due to the loss of eggs, larvae, or maturing and mature fish to the ocean in 1984, or to the inhibitory effect of low salinities on spawning, or to a combination of the latter.

The fact that the 1985 year class of *A. butcheri* was also not caught may reflect a low return of large *A. butcheri* to the estuary by the commencement of the spawning period in 1985. The absence of the 1986, 1987, and 1989 year classes and the paucity of the 1988 year class can probably be attributed to the fact that, although freshwater discharge was not as strong as in 1984, it was still sufficient to breach the bar at the estuary mouth during the spawning period in each of those years (Spurr[6]). It would thus also have been likely to result in a loss to the ocean of eggs and larvae produced during the spawning periods in those years or to the emigration of maturing or mature fish, or in both of these effects (Hodgkin and Clark[5]). The view that heavy freshwater flushing or very low salinities, or both, were the main contributors to the lack of spawning success of *A. butcheri* between 1984 and 1989 is consistent with the observation that, when freshwater discharge was not sufficiently strong to breach the estuary mouth, as was the case between 1990 and 1995 (Spurr[6]), there was at least a reasonable recruitment of each of the 1990 to 1995 year classes.

Comparisons between von Bertalanffy growth parameters for females and males

The likelihood ratio test showed that the growth coefficients (k) for female and male fish were significantly different in only one of the four estuaries, i.e. the Nornalup Walpole Estuary, and even then the probability level was close to 0.05, which is consistent with the fact that the values for the 95% confidence intervals for this parameter for the two sexes overlap in each estuary other than the Nornalup Walpole Estuary. The lack of a marked distinction between the growth rates of female and male fish is hardly surprising because *A. butcheri* undergoes a substantial amount of growth before the gonads start to become mature for the first time (Sarre and Potter, 1999). However, the maximum length and asymptotic length (L_∞) were always greater for female than male fish in each of the four estuaries, thereby paralleling the situation with many other fish species in both southwestern Australia (Laurenson et al., 1994; Wise et al., 1994; Hyndes et al., 1996; 1998) and elsewhere (e.g. Kenchington and Augustine, 1987; McPherson, 1992; Crabtree et al., 1995).

The relatively low values determined for age at length zero for the two sexes in the four estuaries and for males in Lake Clifton, i.e. −0.13 to −0.61 years, reflects in part the good fit of the growth curves to the points for the age at length of the small fish. These low values for t_0 contrast with the −5.21 years for females and −3.70 years for males that were calculated by Morison et al. (1998) for *A. butcheri* in the Gippsland Lakes. Furthermore, the fork lengths at age zero for female and male fish in the Gippsland Lakes were ca. 110 and 100 mm, respectively. Thus, the von Bertalanffy growth equations recorded for *A. butcheri* in the Gippsland Lakes do not provide a good description of the pattern of growth throughout the full size range of fish.

Variations in von Bertalanffy growth parameters among populations

Although the patterns of growth of female and male *A. butcheri* in the Swan River, Wellstead, and Nornalup Walpole estuaries followed the same overall trends, with length increasing rapidly with time initially and then forming asymptotes, the values for k and L_∞ for each sex varied significantly amongst the populations in those estuaries. The initial rate of increase in length in these three estuaries was greatest in the Swan River Estuary and least in the Nornalup Walpole Estuary. Although the value for k for male *A. butcheri* in Lake Clifton differed significantly from that of this sex in the Swan River Estuary, the same was not true for L_∞. However, the value for L_∞ for male *A. butcheri* in Lake Clifton was still similar to that of this sex in the Swan River Estuary. The above comparisons demonstrate that the growth rate in Lake Clifton was similar to that in the Swan River Estuary, which is located only ca. 90 km farther to the north (see also Fig. 1). The von Bertalanffy growth parameters demonstrated that male *A. butcheri* grew more rapidly and attained greater asymptotic lengths in the Swan River Estuary and Lake Clifton than in either the Wellstead or Nornalup Walpole estuaries. The presence of faster growth rates in the Swan River Estuary and Lake Clifton, which are located at latitudes of ca. 32° on the lower west coast of Australia, than in the Nornalup Walpole and Wellstead estuaries, which are situated much farther south at a latitude of ca. 34° on the south coast of Western Australia, may reflect the greater temperatures found in more northern regions.

The pattern of growth of *A. butcheri* in the Moore River Estuary differed from those of this species in each of the other three estuaries and Lake Clifton, in that the increase in length with time was initially slower and the growth curve did not exhibit a marked asymptote. This pattern suggests that some factor or factors were less than optimal for growth during the first few years of life, but that conditions for growth improved later in life. The slow initial rates of increase in length of *A. butcheri* in the Moore River Estuary during early life may be related to the exceptionally high densities of this species in nearshore, shallow waters, the region which constitutes the typical habitat of the juveniles of this species (Sarre, 1999). The far greater density of this species in these waters, than in correspond-

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[6] Spurr, P. 1995. Local resident and former commercial fisherman. Personal commun. Bremer Bay, Western Australia.

ing waters of the other three estuaries, can be gauged from the fact that, during summer, the densities in such waters sometimes reached 234 fish per 250 m² in the Moore River Estuary, whereas they never exceeded 50 fish per 250 m² in any of the other three estuaries. Because *A. butcheri* tends to move into offshore and deeper waters as it increases in size, as is the case with several other fish species in southwestern Australian estuaries (Chubb et al*.,* 1981; Chrystal et al*.,* 1985; Potter et al*.,* 1988; Wise et al*.,* 1994), it then becomes more widely dispersed.

Although the high densities of juvenile *A. butcheri* in nearshore, shallow waters of the Moore River Estuary could have contributed to the initially slow rate at which length increased early in life, it also seems possible that the low salinities, i.e. generally <7‰ (Young et al., 1997), and quality of food in this estuary may also have had an inhibiting influence on the rate at which length increased. The view that low salinity has had such an effect is based on a combination of the results of detailed laboratory trials, which demonstrated that *A. butcheri* did not grow as well at 0‰ and 12‰ as at 24‰ (Sarre et al.[7]) and the fact that the upstream regions of other estuaries, where juvenile *A. butcheri* are located between late spring and early autumn when most growth occurs, are characterized by elevated salinities (Potter and Hyndes, 1994; Sarre, 1999). Although low salinities may restrict growth, it is worth noting that growth in the Wellstead Estuary, which was the only estuary to become hypersaline, was greater than in the Nornalup Walpole Estuary, which is likewise located on the south coast of Western Australia. However, as mentioned earlier, growth in the Wellstead Estuary was not as great as in the Swan River Estuary and Lake Clifton farther to the north.

In the context of potential food, it may be relevant that juvenile *A. butcheri* feed to a greater extent on algae in the Moore River Estuary than in other estuaries. As pointed out by Blaber (1974) during his study of another sparid, *Rhabdosargus holubi*, which likewise ingests a large amount of algal material, the volume of digestible material consumed is small. However, as *A. butcheri* increased in size in the Moore River Estuary, it fed to an increasing extent on whole large bivalves (Sarre et al., 2000), a food source that has a particularly high energy content (Whitfield, 1980).

The age compositions recorded in this paper for *A. butcheri* in different water bodies have been combined with data on reproductive biology to determine the lengths and ages at which black bream typically reach maturity in these systems, i.e. the L_{50} and A_{50} (Sarre and Potter, 1999). The resultant data showed that, amongst the estuarine populations, the A_{50} for female *A. butcheri* was lowest in the Swan River Estuary (2.2 years), in which the growth was greatest, and greatest in the Nornalup Walpole Estuary

(4.3 years), in which early growth was relatively slow and the asymptotic length the least. The minimum legal length (MLL) for the capture of *A. butcheri* in southwestern Australia, i.e. 250 mm, is attained as early as 2.7 years in the Swan River Estuary and as late as 6.5 and 6.8 years in the Nornalup Walpole and Moore River estuaries. Because the MLL is well above the L_{50} for females and males of *A. butcheri* at first maturity in each system, it allows a substantial number of the members of each population to reach maturity before they are likely to be caught by either recreational or professional fishermen. However, the relatively small contribution made by *A. butcheri* ≥5 years old in the heavily fished Swan River Estuary emphasizes the need to keep the upper part of that estuary closed to commercial fishing and suggests that similar measures may be necessary in other estuaries as they become more heavily fished in the future.

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