

Comparisons between generalized growth curves for two estuarine populations of the eel tailed catfish *Cnidoglanis macrocephalus*

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The eel tailed catfishes (Plotosidae) are distributed throughout the Indo-west Pacific region and comprise approximately 30 species. Just over half of these species are found in Australian waters (Hoese and Hanley, 1989). The estuarine catfish or cobbler, *Cnidoglanis macrocephalus* Günther, is one of three plotosid species that are found in the marine and estuarine waters of the southwestern region of Australia (Kowarsky, 1976; Hutchins and Swainston, 1986). *Cnidoglanis macrocephalus* can complete its life cycle in estuaries as well as in coastal marine waters (Laurenson et al., 1993a), suggesting that the populations of this species in each of the different estuaries represent separate demes, a view supported by the results of electrophoretic studies (Ayvazian et al., 1994).

Cnidoglanis macrocephalus is the most valuable of several teleosts fished commercially in Western Australian estuaries (Lenanton and Potter, 1987). While the permanently open Swan and Peel-Harvey estuaries on the southwestern coast

of Western Australia were previously the main contributors to the fishery for this species (Laurenson et al., 1992), this role has now been assumed by Wilson Inlet on the southern coast of the state (Laurenson, 1992; Laurenson et al., 1993b). In contrast to the Swan and Peel-Harvey estuaries, Wilson Inlet is seasonally closed and, because of its more southerly location, does not reach as high a temperature in the summer (c.f. Loneragan et al., 1989; Potter et al., 1993).

Fish are commonly aged by counting the number of annuli on hard structures, such as scales, otoliths, vertebrae, or spines (e.g. Beamish and McFarlane, 1983; Casselman, 1987). However, prior to carrying out such counts, it is important to validate that each of the sequential growth zones is formed annually (e.g. Beamish and McFarlane, 1983; Beckman et al., 1989; Collins et al., 1989; Hyndes et al., 1992). Although Nel et al. (1985) showed that the translucent zones in the asterisci of *C. macrocephalus* from the Swan Estuary tended to be formed annually, their

results were based on pooled data for all fish and, thus, did not verify that this applied equally to each of the sequential translucent zones. Moreover, since the data for males and females were pooled, it was not possible to determine whether the growth rates of the two sexes in this system were the same.

A variety of different forms of growth equations can be calculated from 1) the lengths at given ages and 2) back calculations of body length at each annulus, using the relationship between body length and otolith radius. Both calculations use a predetermined "birth date" for the species. The effectiveness of using length-at-age data relies on obtaining representative samples of all age classes. Back calculations are particularly useful when certain age classes have not been sampled effectively but may produce biased estimates of the lengths of younger fish, i.e. Lee's phenomenon (Ricker, 1975). Furthermore, the lack of independence of the multiple measures for lengths at annulus formation obtained for a single fish by this method may introduce a statistical bias.

The aims of our study were 1) to validate that each of the sequential translucent growth zones on otoliths of *C. macrocephalus* in Wilson Inlet and the Swan Estuary correspond to an annulus and 2) to construct growth curves for each sex in both populations, using both lengths of fish at age of capture and back-calculated lengths. These curves were then used to compare a) growth between sexes within each estuary, b) growth between estuaries, and c) growth calculated using lengths at age and back-calculated lengths.

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Materials and methods

Collection of fish

Juvenile and adult *Cnidogobius macrocephalus* were collected by seining at eight sites, gillnetting at nine sites, and otter trawling at six sites located throughout the basin of Wilson Inlet between September 1987 and April 1989 (see Fig. 1 in Potter et al. [1993] for location of this estuary and the sampling sites). Some of the sampling by each method was carried out monthly, while the rest was undertaken bimonthly (see Potter et al., 1993). The seine was 41.5 m long (stretched mesh = 51 mm in wings and 9.5 mm in pocket), while the gill net consisted of six 30-m contiguous panels, each with a different stretched mesh size, i.e. 38, 51, 63, 76, 89, or 102 mm. The stretched mesh in the wings and codend of the otter trawl were 51 and 25 mm, respectively. Seine netting and otter trawling were carried out during the day, while gillnetting was undertaken overnight. A small number of larval and post-larval *C. macrocephalus* were also collected in night-time plankton tows (Neira and Potter, 1992) and from their nests by dip net (Laurenson et al., 1993a).

Sampling in the Swan Estuary employed winged funnel traps between August 1982 and April 1983 (see Nel et al., 1985). Fish were also taken in a seine and otter trawl similar to those used in Wilson Inlet and with gill nets containing panels with the same mesh sizes as those employed in Wilson Inlet, but with additional panels of 13- and 25-mm mesh.

Validation of translucent zones as annuli and otolith measurements

The first 10 males and 10 females of *C. macrocephalus* caught in each panel of the gill nets at each site in Wilson Inlet on each sampling occasion, together with all fish caught in seine nets, were kept for ageing. All fish caught in otter trawls, except for a small number that were retained for tagging experiments, were also used for ageing. The total length and wet weight of each fish were recorded to the nearest 1 mm and 0.1 g, respectively. Each *C. macrocephalus* was sexed, except in the case of smaller fish (<ca. 100 mm) where the gonad could not be distinguished as either ovary or testis. The small, round asterisci and the larger, elongate lapilli otoliths were removed from fish and stored dry in envelopes.

Because preliminary examination showed that translucent zones were more clearly detectable in the lapilli than asterisci of *C. macrocephalus* from Wilson Inlet, lapilli were used for ageing this species in Wilson Inlet. The lapilli were placed in a bath of methyl salicylate and viewed under reflected light

against a dark background with a dissecting microscope. The number of translucent zones on each otolith was recorded. Because the outermost opaque region of the otolith was not sharply defined, it was difficult to obtain consistent measurements of the distance between the outer translucent zone and the edge of the otolith. The mean monthly trends shown by the width of this marginal increment did not follow a very consistent pattern and therefore could not be used to establish that the outer zones on these otoliths were formed annually (see Maceina et al., 1987; Hyndes et al., 1992). To provide an alternative method for validating that each of the translucent zones corresponded to an annulus, the percentage of lapilli with a clearly defined translucent zone at the periphery of the otolith in each month was calculated separately for otoliths with one, two, three, four, and five or more inner translucent zones (e.g. Crozier, 1989; Beckman et al., 1990).

The difficulty in obtaining consistent measurements of the marginal increments in the lapilli of *C. macrocephalus* from Wilson Inlet was not encountered with the asterisci of this species from the Swan Estuary (Nel et al., 1985). The measurements of asterisci and total lengths of *C. macrocephalus* from the Swan Estuary were obtained from the raw data used by Nel et al. (1985). When two or more translucent zones were present, the relative values for the marginal increment were obtained by expressing the distance between the outer edge of the outermost translucent zone and the edge of the otolith as a percentage of the distance between the outer edges of the two outermost translucent zones. When only one translucent zone was present, the relative values were expressed as a percentage of the distance between the outer edge of the outermost translucent zone and the nucleus. The mean relative marginal increments are subsequently referred to as mean marginal increments. The distances between the nucleus of the otolith and the outer edge of each translucent zone and the outer edge of the otolith were measured to the nearest 0.05 mm along the long axis of lapilli and asterisci otoliths from Wilson Inlet and Swan Estuary, respectively.

Calculation of growth curves

The relationships $g(x)$ between the natural logarithms of total length (y) and lapillus radius (x) of *C. macrocephalus* in Wilson Inlet, and between the natural logarithms of total length and asteriscus radius of this species in the Swan Estuary, were described by a third order polynomial of the form $y = a + bx + cx^2 + dx^3$, where a , b , c , and d are constants. Back calculations of fish length at the formation of

each annulus followed a body proportional hypothesis (Francis, 1990), using the equation $L_i = L \exp[g(\ln(S_i)) - g(\ln(S))]$, where L_i is the estimated total length at the formation of the i th annulus, L is the total length at capture, S_i is the radius of the i th annulus, and S is otolith radius.

Lengths at age and back-calculated lengths were used to construct growth curves using the traditional form of the von Bertalanffy equation, $L_t = L_\infty(1 - \exp[-k(t - t_0)])$, where L_t is the mean body length of fish of age t , L_∞ is the asymptotic mean length of fish in the population, t_0 is the theoretical age at which the length of fish is zero, and k is the growth coefficient. Since the von Bertalanffy curves failed to describe adequately the full range of data (see Discussion), the more flexible growth curve equation derived by Schnute (1981) was fitted to the data. There are four possible forms of this equation, depending on the values of the parameters a and b , where y_1 and y_2 are the lengths of the fish at the specified ages T_1 and T_2 (i.e. ages 1 and 4, which bounded the majority of the data set in this application).

$$\text{Case 1: } a \neq 0, b \neq 0 \quad L_t = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - \exp(-a(t - T_1))}{1 - \exp(-a(T_2 - T_1))} \right]^{1/b};$$

$$\text{Case 2: } a \neq 0, b = 0 \quad L_t = y_1 \exp \left[\log \left(\frac{y_2}{y_1} \right) \frac{1 - \exp(-a(t - T_1))}{1 - \exp(-a(T_2 - T_1))} \right];$$

$$\text{Case 3: } a = 0, b \neq 0 \quad L_t = \left[y_1^b + (y_2^b - y_1^b) \frac{t - T_1}{T_2 - T_1} \right]^{1/b};$$

$$\text{Case 4: } a = 0, b = 0 \quad L_t = y_1 \exp \left[\log \left(\frac{y_2}{y_1} \right) \frac{t - T_1}{T_2 - T_1} \right].$$

When $a > 0$ and $b = 1$, the generalized growth curve is equivalent to the traditional form of the von Bertalanffy growth curve, with $a = k$. The resultant form of the generalized growth equation was determined by the parameters a and b that resulted in the minimum sum of squared deviations. Data were fitted by using a nonlinear least squares method, employing the nonlinear (NLIN) procedure of SAS (Ihnen and Goodnight, 1987). All back calculations and curve fittings were carried out separately for each sex in both populations. Juveniles, for which the sex could not be determined, were included in calculating growth curves of both sexes from length-at-age data. Calculations of all curves assumed a birth date of 1 December in Wilson Inlet and 1 November in Swan Estuary (Laurenson et al., 1993a).

Each growth curve, fitted by using the traditional form of the von Bertalanffy growth equation, was compared with the corresponding generalized growth curve by using a likelihood ratio test, an approach adopted with several other fish species (Kimura, 1980; Kirkwood, 1983; Cerrato, 1990; Hampton, 1991; Buxton, 1993). The generalized growth curves of both sexes in Wilson Inlet and Swan Estuary based

on lengths at age and back calculated lengths, were compared by using the same likelihood ratio test, which involved determining the improvement of fit obtained by using the two separate curves, rather than a common curve. This involved 1) comparing the curve for males with that for females in each system, using first lengths at age and then back-calculated lengths; 2) comparing the curves for each sex in Wilson Inlet with that for the corresponding sex in Swan Estuary, using first lengths at age and then back-calculated lengths; and 3) comparing the curves calculated from lengths at age with those obtained from back-calculated lengths, first for males in each system and then for females in each system.

Results

Mean monthly percentages of otoliths from Wilson Inlet with a peripheral translucent zone and one, two, or three inner translucent zones followed similar seasonal trends (Fig. 1). The percentage of such otoliths rose sharply in early spring and fell to close to zero in the late spring or early summer where they

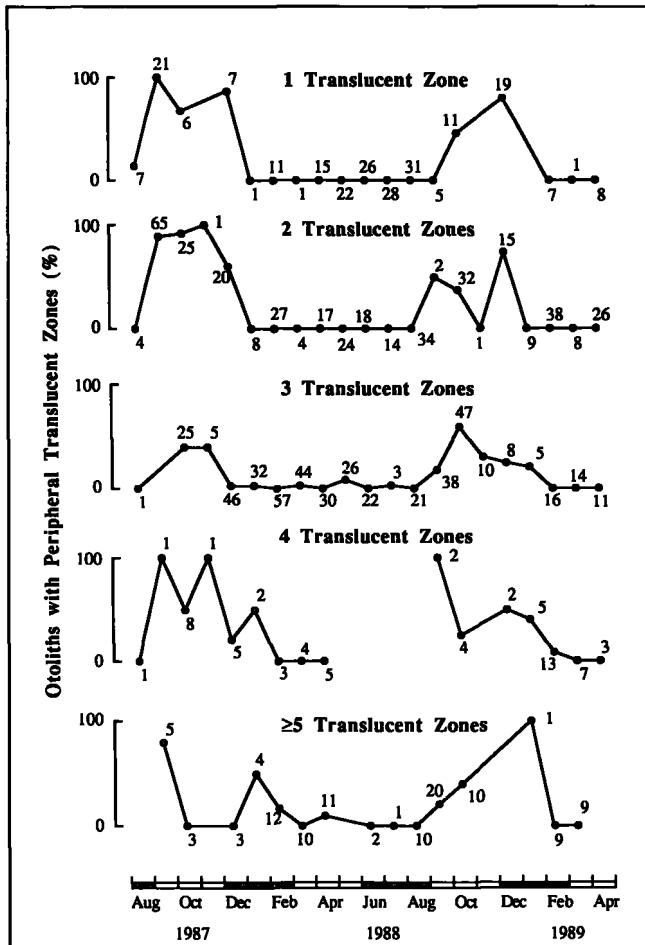


Figure 1

The percentage of lapilli of the eel tailed catfish *Cnidoglanis macrocephalus* from Wilson Inlet possessing a clearly defined peripheral translucent zone in each month. Data are presented separately for otoliths in which there are one to five or more inner translucent zones. Black rectangles on the x-axis represent summer and winter months, white rectangles the autumn and spring months.

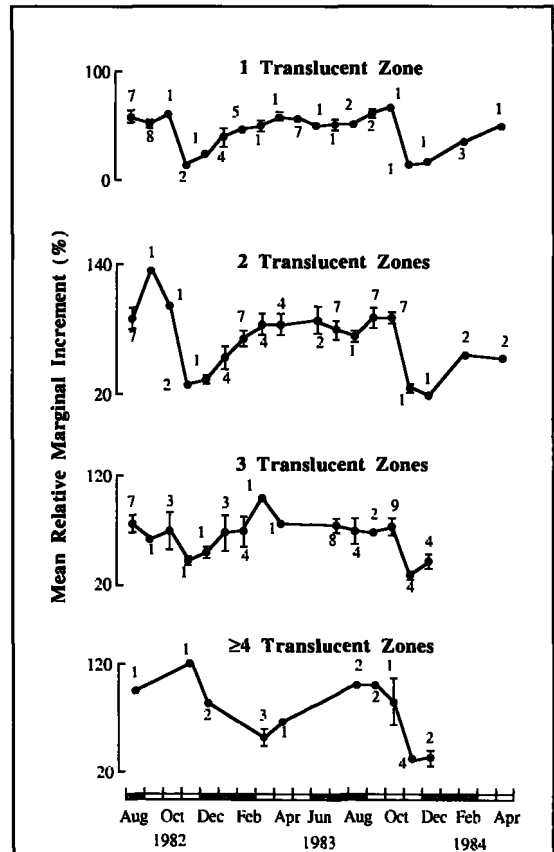


Figure 2

Mean relative marginal increments for asterisci otoliths of the eel tailed catfish, *Cnidoglanis macrocephalus* from the Swan Estuary. Recalculated from the data used by Nel et al. (1985). Data are presented separately for otoliths in which there are one to four or more translucent zones. Standard errors are given when sample size was ≥ 3 . Black rectangles on the x-axis represent summer and winter months, white rectangles the autumn and spring months.

remained through the following summer, autumn, and winter months. Although data for otoliths with both four and five or more translucent zones were less abundant, they followed a similar trend (Fig. 1). The mean marginal increment on otoliths with one, two, and three translucent zones from Swan Estuary fell to a minimum in the spring and rose progressively during the ensuing summer and early autumn, before levelling off in the late autumn and winter (Fig. 2). While the number of otoliths with four or more translucent zones was small, the trend shown by the marginal increment on these otoliths is similar.

A cubic polynomial equation, using logarithm (natural) transformed data, provided the best description of the relationship between otolith radius and total fish length in both Wilson Inlet and Swan Estuary, when lapilli and asterisci otoliths were used, respectively (Fig. 3).

The equations were as follows:

Wilson Inlet

Males: $y = 5.700 + 1.388x - 0.191x^2 - 0.315x^3$ ($R^2 = 0.935, P < 0.001, n = 462$)
 Females: $y = 5.708 + 1.374x - 0.235x^2 - 0.317x^3$ ($R^2 = 0.926, P < 0.001, n = 876$)

Swan Estuary

Males: $y = 6.152 + 0.951x - 0.875x^2 - 0.400x^3$ ($R^2 = 0.931$, $P < 0.001$, $n = 499$)

Females: $y = 6.174 + 1.171x - 0.479x^2 - 0.230x^3$ ($R^2 = 0.931$, $P < 0.001$, $n = 568$)

Examination of the otoliths suggests that the curvilinearity at the upper end of these relationships (Fig. 3) is due to the otoliths of larger fish tending to thicken rather than lengthen.

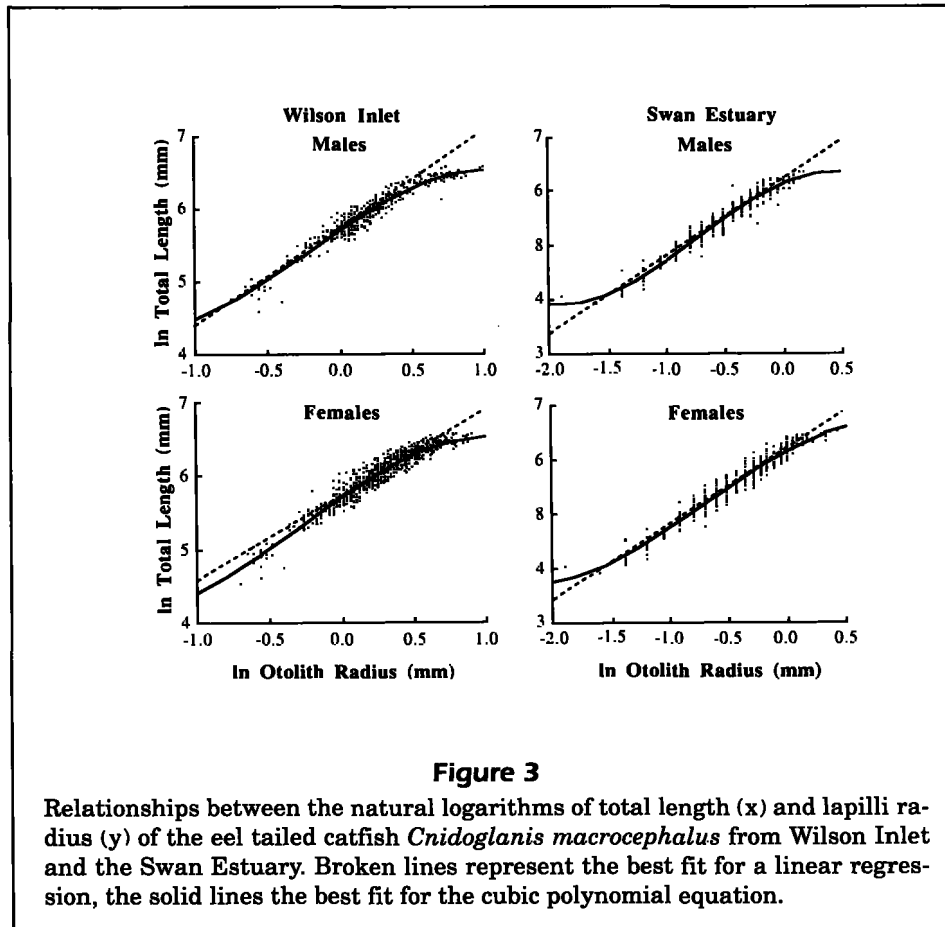
The lengths of fish of a given age class were highly variable (Figs 4 and 5). For example, the lengths of female fish that were about four years old in Wilson Inlet ranged from 478 to 631 mm and those that were about three years old in the Swan Estuary ranged from 351 to 591 mm. The predicted lengths of fish, derived from generalized growth curves, were greater when lengths at age rather than back-calculated lengths were used for fish of ages 1 and 2 (Table 1). The high values for R^2 for the generalized growth curves, derived from both lengths at age and back-calculated lengths, show that these curves fit the data well (Table 2). The oldest male and female *C. macrocephalus* caught in Wilson Inlet were 12³/₄ years old (718 mm, 1885 g) and 9³/₄ years old (670 mm, 1738 g), respectively. The corresponding values

for fish from the Swan Estuary were 5 years (582 mm, 1142 g) and 6³/₄ years (683 mm, 1880 g), respectively.

The use of common curves in the cases of both lengths at age and back-calculated lengths for each of the two sexes in each system accounted for 89 to 94% of the observed variance. By assuming that a difference exists between the growth curves of the two sexes in each system and with each of the two methods, the fit was improved by only 0.003% for back calculated data for the Swan Estuary and 0.3% for length at age data for Wilson Inlet.

Applying likelihood ratio tests, the length-at-age growth curves for males and females differed significantly in both the Wilson Inlet ($P < 0.001$) and Swan Estuary populations ($P < 0.05$). Back-calculated growth curves calculated for the two sexes also differed significantly ($P < 0.001$) in Wilson Inlet but not in Swan Estuary.

The use of a common curve for each sex by using both lengths at age and back-calculated lengths for



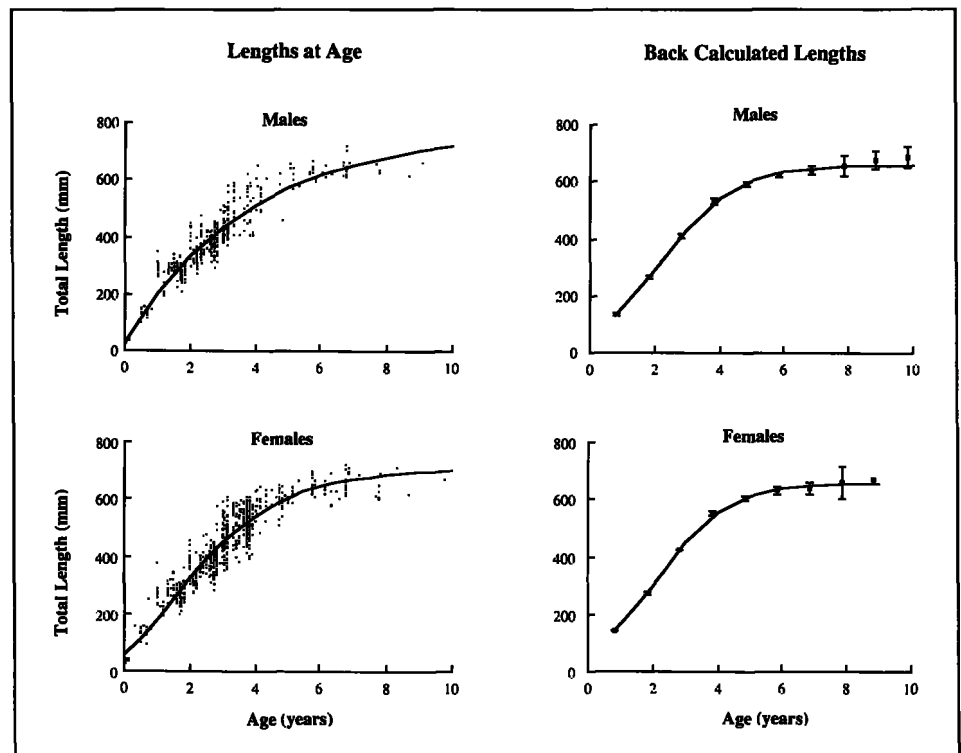
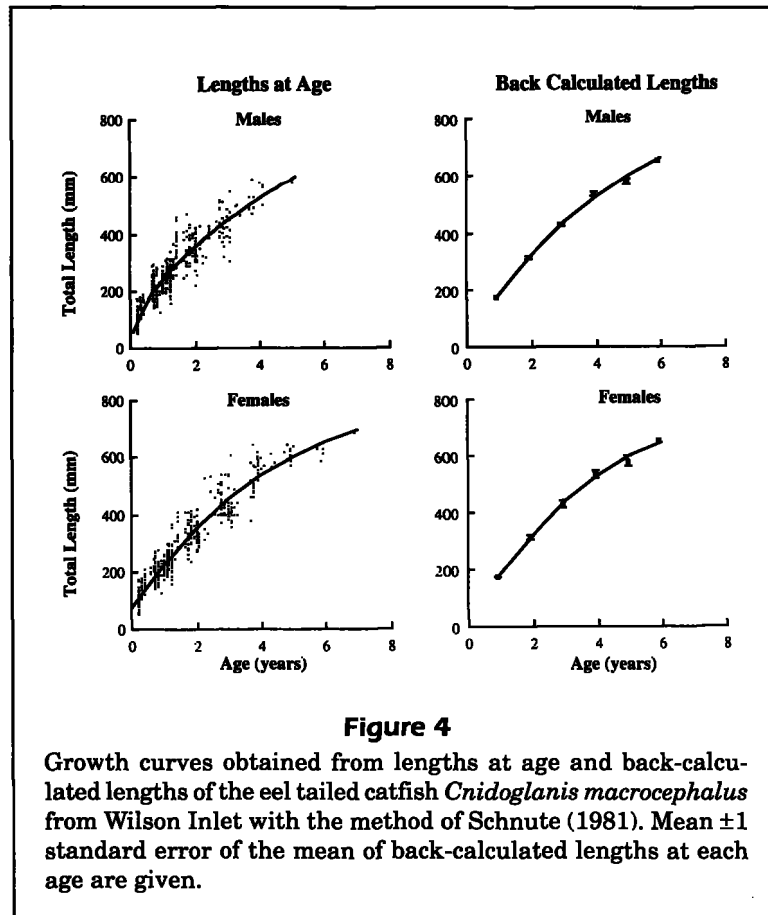


Table 1

The total lengths (mm) at sequential ages of the eel tailed catfish *Cnidoglanis macrocephalus* in Wilson Inlet and Swan Estuary, predicted from generalized growth curves (Schnute, 1981) calculated from lengths at age (LAA) and back-calculated lengths (BCL).

Age	Wilson Inlet				Swan Estuary			
	Male LAA	Female LAA	Male BCL	Female BCL	Male LAA	Female LAA	Male BCL	Female BCL
1	203	180	156	158	239	225	185	184
2	335	324	293	298	356	353	324	323
3	436	449	436	448	447	456	436	440
4	513	541	543	556	525	538	527	531
5	573	603	605	613	594	603	601	598
6	619	643	636	638		654		647
7	655	668	650	648		694		
8	682	684	657	652				
9	703	693	660	653				
10	720	699	661					

Table 2

The parameters of the generalized growth curves fitted to lengths at age and back-calculated lengths for the eel tailed catfish *Cnidoglanis macrocephalus* in Wilson Inlet and Swan Estuary. y_1 and y_2 are lengths (mm) at reference ages 1 and 4 and a and b are the parameters of the growth equation.

Location			y_1	y_2	a	b	R^2	n
Wilson Inlet	Lengths at age	Female	180	541	0.51	0.20	0.90	916
		Male	203	513	0.26	1.04	0.92	502
	Back-calculated lengths	Female	158	556	0.96	-0.99	0.94	2354
		Male	156	543	0.82	-0.71	0.96	1102
Swan Estuary	Length at age	Female	225	537	0.25	0.90	0.91	517
		Male	239	525	0.02	1.75	0.85	447
	Back-calculated lengths	Female	183	530	0.37	0.53	0.90	615
		Male	184	527	0.20	1.04	0.85	426

the populations in the two systems accounted for 90 to 94% of the observed variance. The additional variance explained by assuming a difference between the growth curves for each sex in each system improved the fit to the four data sets by 0.3 to 0.6%. The growth curves estimated for males from lengths at age and from back-calculated lengths in Wilson Inlet differed significantly from those estimated for males in Swan Estuary using the corresponding types of data; the same was true for females ($P < 0.001$).

The percentage of the variance explained by the common curves derived from lengths at age and back-calculated lengths for each sex in each system ranged from 81% for males in the Swan Estuary to 94% for both males and females in Wilson Inlet. The percentage of the variance explained by assuming that the growth curves determined from lengths at age and

back-calculated lengths are different was improved by 0.8 and 0.2% respectively for males and females from Wilson Inlet and by 4.2 and 1.6% respectively for males and females from the Swan Estuary. The length at age and back-calculated growth curves for males in Wilson Inlet and Swan Estuary differed significantly; the same applied for females ($P < 0.001$).

Discussion

The present study of the lapilli of *C. macrocephalus* in Wilson Inlet is the first to demonstrate in a plotosid that each of the otolith's first four translucent zones, and probably all other translucent zones, are formed annually. Furthermore, re-analysis of the data of Nel et al. (1985) has shown that this also applies to the

asterisci in *C. macrocephalus* from the Swan Estuary. The importance of confirming that each successive translucent zone is formed annually is demonstrated by the results obtained by Hyndes et al. (1992) for whole sagittae of *Platycephalus speculator* in Wilson Inlet. In that species, mean monthly marginal increments showed a very clear seasonal trend when individual marginal increments on all unsectioned otoliths were pooled, irrespective of the number of translucent zones. However, they did not show conspicuous trends when the data for the marginal increments on unsectioned otoliths with two, three, four, and five or more translucent zones were each plotted separately. In other words, when marginal increment data for all otoliths were pooled, the pronounced seasonality exhibited by the mean marginal increments on otoliths with one translucent zone of *P. speculator* had an overwhelming influence on the data set.

The von Bertalanffy growth curve did not sufficiently describe the growth of *C. macrocephalus* from Wilson Inlet; the lengths were consistently greater than the mean length at ages 7 and above and showed increasing divergence with age. This was far less of a problem in Swan Estuary where older fish were less abundant. The generalized growth curve provided better fits to the data than the von Bertalanffy curve for males and females in both systems, when both lengths at age and back-calculated lengths were used. Furthermore, likelihood ratio tests showed that this improvement was significant in three of the four cases for the population in Wilson Inlet. Such improvement is consistent with the observation that when there is an acceleration of growth early in life, the von Bertalanffy growth curve does not provide as adequate a fit as the Schnute, Gompertz, or Richard's curves (Schnute, 1981; Campana and Jones, 1992).

While the presence among younger fish of smaller back-calculated lengths than mean lengths at age (Table 1) would be consistent with Lee's phenomenon (Ricker, 1975), it could also have been brought about by the low numbers of younger fish in the samples. The fits of the common curves constructed for each sex in Wilson Inlet from lengths at age and back-calculated lengths were improved by only 0.2% for females and 0.8% for males when separate curves were used. However, this was not the case for fish in the Swan Estuary, where the sum of squares was improved by 1.6% for females and by as much as 4.2% for the males. The differences in improvement in fit in the two systems probably reflects the fact that, while the 0+ age class in the Swan Estuary was caught in greater numbers, it tended to be represented in samples by the larger members of this age class.

The improvement of fit obtained by using separate growth curves was small, both in comparisons between males and females in Wilson Inlet and Swan Estuary and in comparisons between corresponding sexes in the two systems. This applied to curves constructed both from lengths at age and back-calculated lengths. In none of these cases was the sum of squares improved by more than 0.6%. However, although the differences between the curves for each sex in each system and for the corresponding sexes in the two populations were small, and even though the lengths varied considerably at a given age, the curves were still statistically different with a likelihood ratio test (usually $P < 0.001$). These differences probably reflect the influence of the large number of data points used to construct the growth curves.

The small magnitude of the differences between these growth curves is demonstrated by the fact that at age 4, the lengths of males and females in Wilson Inlet and the Swan Estuary, predicted from the generalized growth curve, generally differed by less than 3%, irrespective of whether the curve was constructed from lengths at age or back-calculated lengths. Thus, although there were usually highly statistically significant differences between curves, the actual differences between the curves for the two sexes in each population and between the corresponding sexes in those populations are almost certainly of limited biological significance.

In conclusion, the growth of *C. macrocephalus* in Wilson Inlet was similar to that in the Swan Estuary. This similarity occurred despite the fact that water temperatures in the latter system were over 5°C higher in the summer (c.f. Loneragan and Potter, 1990; Potter et al., 1993). Wilson Inlet is eutrophic and therefore more productive (Lukatelich et al., 1987) and consequently contains a greater abundance of the large deposit-feeding benthic invertebrates¹ that make a major contribution to the diet of *C. macrocephalus* (Nel et al., 1985; Laurenson, 1992). Therefore the similarity between the growth rate of *C. macrocephalus* in Wilson Inlet and the Swan Estuary may reflect a compensation for lower water temperatures by greater prey abundance.

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¹ Platell, M. School of Biological and Environmental Sciences, Murdoch Univ., Murdoch, Western Australia 6150, Australia. Personal commun., 1991.

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