Factors influencing growth of *Acanthopagrus butcheri* (Sparidae) in a eutrophic estuary have changed over time

Alan Cottingham, Norman G. Hall, Ian C. Potter

PII: S0272-7714(15)30121-9
DOI: 10.1016/j.ecss.2015.10.031
Reference: YECSS 4934

To appear in: *Estuarine, Coastal and Shelf Science*

Received Date: 17 July 2015
Revised Date: 25 September 2015
Accepted Date: 29 October 2015

Please cite this article as: Cottingham, A., Hall, N.G., Potter, I.C., Factors influencing growth of *Acanthopagrus butcheri* (Sparidae) in a eutrophic estuary have changed over time, *Estuarine, Coastal and Shelf Science* (2015), doi: 10.1016/j.ecss.2015.10.031.

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.
Factors influencing growth of *Acanthopagrus butcheri* (Sparidae) in a eutrophic estuary have changed over time.

Alan Cottingham\(^\text{a,}\)^*, Norman G. Hall\(^\text{a,b}\), Ian C. Potter\(^\text{a}\)

\(^\text{a}\) Centre for Fish and Fisheries Research, School of Veterinary and Life Sciences, Murdoch University, 90 South Street, Murdoch, Western Australia 6150.
\(^\text{b}\) Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Post Office Box 20, North Beach, Western Australia 6920.

*Corresponding author: E-mail address: a.cottingham@murdoch.edu.au, Ph. +61 8 9239 8808

**ABSTRACT**

The overall growth of *Acanthopagrus butcheri* in the eutrophic Swan River Estuary has previously been shown to decline between 1993-95 and 2007-11. This was attributed to the effects of an increase in hypoxia on *A. butcheri* in deeper water, brought about by reductions in freshwater flushing, and to density-dependent effects as this species became concentrated in the better-oxygenated, nearshore shallow waters. In the present study, a year-effect model was developed that provided a good fit to the lengths at age and could thus be used to explore the following: 1) The extent to which somatic growth of *A. butcheri* differed between years in the above two periods and within the later period, which was extended to include data for 2012 to 2014, and 2) whether annual growth in 2007-14 was related to temperature and/or freshwater discharge. Annual length increments for females and males during the second year of life, predicted from the model using a common initial length, were almost invariably less in each year in 2007-14 than in 1993-95. In 2007-14, these predicted increments varied by ~2 times for both females and males and were positively correlated with average temperature during the main growth phase of *A. butcheri*. They were not significantly correlated, however, with freshwater discharge in the preceding cool wet ‘winter’ months, when the vast majority of rainfall occurs. The demonstration that the growth of *A. butcheri* was positively correlated with temperature for years in the latter period is consistent with the metabolic theory of ecology and contrasts with
growth declining between 1993-95 and 2007-14 when temperatures were increasing. Thus, any influence of temperature on growth between those periods was overridden by other factors, i.e. hypoxia and increased densities. As *A. butcheri* completes its life cycle within its natal estuary and has plastic biological characteristics, it is an ideal candidate for use as an indicator of the health of an estuary and for hypothesising on the effects of climate change on fish species.

Keywords: Estuarine fish species; inter-annual variations in growth; temperature; freshwater discharge; hypoxia; density-dependence

1. Introduction

An understanding of the growth of individuals in a fish stock is crucial for determining the status of that stock and thus for assessing its resilience to fishing pressure (Beverton & Holt, 1957; Quinn & Deriso, 1999; Haddon, 2011). The growth of fish in a population is typically described by fitting a von Bertalanffy growth model to the lengths at age of individuals in that population, using pooled data for several years (Ricker, 1979; Quinn & Deriso, 1999; Jennings *et al.*, 2009). This enables the expected lengths at age of fish overall to be estimated for the period for which lengths and ages were recorded, irrespective of the extent to which growth varied among years.

The overall von Bertalanffy growth curves of the females and males of the Black Bream *Acanthopagrus butcheri* in the Swan River Estuary in south-western Australia in 1993-95 were compared with those in 2007-11 (Cottingham *et al.*, 2014). This showed that, overall, the growth of this estuarine species was less in the latter period, when environmental conditions had declined through detrimental effects caused by reductions in freshwater discharge, brought about by declining rainfall. These detrimental effects included a pronounced increase in the extent of hypoxia in deeper water, which, on the basis of other studies, would presumably have inhibited the growth of those fish that remained within those waters (Pichavant *et al.*, 2000, 2001; Eby *et al.*, 2005). The increases in hypoxia also led, however, to larger *A. butcheri* tending to move from deeper waters into the shallow and better oxygenated waters, where, as a consequence,
densities increased markedly, but subsequently remained relatively constant through 2007-11. It was thus proposed that density-dependent effects contributed to the reduction in the growth of *A. butcheri* that occurred in the intervening years between 1993-95 and 2007-11. As this reduction occurred when temperatures were increasing (Australian Bureau of Meteorology, 2015), and growth would thus have been expected to increase (Brown *et al.*, 2004), any positive influence of temperature was overridden by those other effects.

Relatively few studies have explored the extent to which the growth of individuals of an estuarine species, *i.e.* whose life cycle is completed within the estuary (Potter *et al.*, 2015), varies either between or within periods in a given system and is related to certain environmental variables. The results of those few studies in temperate estuaries, which typically used a mixed-modelling approach to relate annual growth increments in otoliths to selected environmental variables, varied with region and between species. While such growth in *A. butcheri* was thus found to be negatively correlated with temperature in a suite of estuaries in Tasmania, it was positively correlated with that environmental variable in an estuary in South Australia, where climatic conditions are very different (Doubleday *et al.*, 2015). As with *A. butcheri* in South Australia, otolith growth of the Estuary Perch *Percalates colonorum* in Victoria, further east in southern Australia, was positively correlated with temperature and, in this case, to a greater extent than any other variable examined (Morrongiello *et al.*, 2014). The growth of the otoliths of *A. butcheri* in South Australia were positively correlated with rainfall but, surprisingly, not with freshwater discharge (Doubleday *et al.*, 2015), whereas the growth of the otoliths of *P. colonorum* in Victoria was correlated with freshwater discharge, but not as strongly as with temperature (Morrongiello *et al.*, 2014). In contrast, analyses of annual increments in otoliths and back-calculations of length at age demonstrated that the growth of the Spotted Seatrout *Cynoscion nebulosus* in San Carlos Bay, Florida, was positively correlated with salinity and thus negatively with freshwater discharge (Bortone *et al.*, 2006).
Each of the above studies assumed a proportionality between annual increments in body length and otolith size, either explicitly, e.g. Bortone et al. (2006), or when drawing inferences regarding growth in length at age from otolith growth (Morrongiello et al., 2014; Doubleday et al., 2015). The results of several studies suggest, however, that, at least in some species, direct coupling does not occur, with, for example, otoliths continuing to grow after growth in body size has largely or entirely ceased and sometimes respond to environmental factors in different ways than body size (e.g. Fey, 2006; Wilson et al., 2009; Réveillac et al., 2015).

No study has used an appropriate model, fitted to length-at-age data, to explore the extents to which, in terms of body size, the growth of an estuarine fish species varies among years. In the case of the lacustrine species Coregonus hoyi, Szalai et al. (2003) described the lengths at age, using a von Bertalanffy growth curve with time-varying \( L_\infty \) and assuming a linear relationship with \( k \), to predict the length increments of each age class in successive years and thereby accounted for inter-annual variations in growth. He & Bence (2007) later extended that model, for another lacustrine species, to allow each year-specific von Bertalanffy growth parameter to vary over time.

The first aim of this study was to develop a model that would enable the extent to which the somatic growth of A. butcheri in the Swan River Estuary varies among years to be estimated. A year-effect model, based on but less complex than that of He & Bence (2007), was thus developed to accommodate the characteristics of the data obtained for A. butcheri (see Materials and Methods). The results were used to determine how annual increments in body length of A. butcheri in the Swan River Estuary varied among years in 1993-95 and 2007-14, the latter period encompassing the years in 2007-11 for which the average, but not annual, growth had previously been determined (Cottingham et al., 2014). The model thus enabled the following hypotheses regarding A. butcheri in the Swan River Estuary to be explored. 1) Annual somatic growth was consistently less in each year in 2007-14 than in each year in 1993-95. 2) Since the densities in
2007-14 had stabilised in shallow waters, where the majority of *A. butcheri* then resided, annual somatic growth of their younger individuals is positively related to temperature, as is typical of fish species within their normal temperature range (Angilletta *et al*., 2010; Neuheimer *et al*., 2011) and of the otoliths of *A. butcheri* and *P. colonorum* further east on mainland Australia (Morrongiello *et al*., 2014; Doubleday *et al*., 2015). 3) The question of whether somatic growth in 2007-14 was related to freshwater discharge, which occurs predominantly in the non-growth period of mid-winter to early spring, was examined. Finally, the observed lengths at age for the years in 1993-95 and 2007-14 periods, and those for more fragmentary data for some intermediate years, were used to elucidate how the pattern of growth of *A. butcheri* in the Swan River Estuary changed over more than two decades, during which this system was subjected to severe anthropogenic perturbations.

2. Materials and methods

2.1. Sampling regime

*Acanthopagrus butcheri* was sampled at nine sites in the upper Swan River Estuary (Fig. 1). Nearshore, shallow waters were sampled using 21.5 and 41.5 m long seine nets in each season between spring 2007 and winter 2011. Offshore waters were sampled by gill netting in waters adjacent to each seine net site. Gill netting was undertaken at the same time (season) as seine netting between spring 2007 and winter 2009, after which it was discontinued as it was catching few fish. *Acanthopagrus butcheri* was also caught at intervals between the spring and following winter in 2011 to 2014 using seine and gill nets in the same region of the upper Swan River Estuary as the above nine sampling sites.

The 21.5 m seine net, which consisted of a 1.5 m wide bunt of 3 mm mesh and two 10 m long wings (each comprising 4 m of 3 mm mesh and 6 m of 9 mm mesh), swept an area of 116 m$^2$, while the 41.5 m seine net, which contained a 1.5 m wide bunt made of 9 mm mesh and two 20 m long wings comprising 25 mm mesh, swept an area of 274 m$^2$. The 21.5 m seine net was laid parallel to the bank and then hauled onto the shore, whereas the 41.5 m seine was deployed
in a semi-circle from the bank using a small boat and then likewise hauled on to the shore. The gill net, which comprised eight 20 m long panels, each with a different stretched mesh size, *i.e.* 38, 51, 63, 76, 89, 102, 115 and 127 mm, was set, just after sunset, parallel to the shore in water depths of 2 to 6 m and retrieved 3 h later.

*Acanthopagrus butcheri* had previously been caught in the upper Swan River Estuary between spring 1993 and winter 1995 by using the 41.5 m long seine net at six of the above nine sites in nearshore, shallow waters, and by employing a gill net (comprising panels of the same dimensions and mesh sizes as described above) at all nine sites in offshore waters (Sarre & Potter, 2000).

Throughout the subsequent text, each of the 12 months between the spring of one year and the winter of the next year (which thus commences when *A. butcheri* spawns) is subsequently referred to as a ‘year’, *e.g.* spring 2008 to winter 2009 is referred to as 2008/09. Note that there were continuous data for the spring to winter seasons in the seven ‘years’ from 2007/08 to 2013/14, which were used for intra-period comparisons.

### 2.2. Temperature and freshwater flow

Annual mean maximum air temperatures, recorded between 1990 and 2014 at Perth Airport in the vicinity of the Swan River Estuary were taken from the website of the Australian Bureau of Meteorology (2015). A linear equation was used to describe the relationship between these temperatures and years. A one-tailed t-test was then employed to determine whether the Pearson’s correlation coefficient relating temperature to year was statistically significant and thus confirm that air temperature increased over that period. Annual freshwater discharge entering the Swan River Estuary at gauging station 616011, upstream of the study area, in each year between 1990 and 2014 was taken from the website of the Western Australian Department of Water (2015). A log-linear equation was used to describe the curvilinear relationship between
freshwater discharge and year. Back-transformed predicted values for freshwater discharge were corrected to account for the bias associated with log transformation (Beauchamp & Olson, 1973). A one-tailed t-test was employed to determine whether Pearson’s correlation coefficient between the log-transformed values of freshwater discharge and year was statistically significant and thereby confirm that, as previously shown for 1992 to 2011 (Cottingham et al., 2014), annual freshwater discharge declined between 1990 and 2014.

2.3. Growth

Following their capture, *A. butcheri* were euthanised in an ice slurry and transported to the laboratory where they were sexed and their total length measured to the nearest 1 mm. The whole otoliths of all *A. butcheri* were initially examined using a dissecting microscope under reflected light and their opaque zones counted. When the number of opaque zones was ≤6, that number was recorded, whereas, when it was >6, the otolith was sectioned and the number of its opaque zones then recorded (for rationale see Sarre & Potter (2000)). For sectioning, each otolith was embedded in clear epoxy resin, sectioned transversely (*ca* 400 µm thickness) through its primordium and mounted on a glass microscope slide and again viewed under reflected light. N.B. Marginal increment analyses by Sarre & Potter (2000) validated that the opaque zones in the otoliths of *A. butcheri* in the Swan River Estuary are typically formed annually. Each fish was aged, using the number of opaque zones in one of its otoliths, the date of capture and an approximate birth date (defined as the date approximating to the peak in gonadosomatic index, *i.e.* 1 October) of this species in this estuary, together with knowledge that the new opaque zone typically becomes delineated from the periphery of the otolith by the beginning of November.

2.3. Year-effect growth model

The year-effect growth model, developed in this study, has essentially the same structure as that of He & Bence (2007) and thus, when estimating the parameters associated with the growth that takes place during each year, likewise takes into account the length of each age class at the
commencement of each year. In contrast to He & Bence (2007), however, our samples were collected throughout the year, rather than within a very restricted period each year, and were obtained using both seine and gill nets, rather than just gill nets, and thereby contained fish in the earlier years of life, when growth is most rapid. Our model thus differed from that of He & Bence (2007) as follows. (1) The model predicts lengths at decimal ages, rather than at annual intervals. (2) Deviations from the growth curve are assumed to be normally-distributed, and thus the predicted lengths at age represent the mean rather than median length at age. (3) Parameters include the lengths at age of each year-class (except that of the 0+) at the start of the sampling period during which fish were collected, rather than parameters for the lengths of fish at a specific age, i.e. 3 years old. (4) The lengths at age zero for fish that entered the population in the first and subsequent years of sampling are calculated using the von Bertalanffy growth equation and the growth parameters for that year. Our model was fitted by maximising the log-likelihood rather than employing a hierarchical Bayesian approach.

The modified year-effect model was used to calculate, separately for each sex, year-specific growth parameters and expected lengths at different ages in each year. As a single growth model could not be fitted to the entire series, due to gaps in the data, the year-effect model was fitted first to the lengths at age of fish collected during 1993/94 and 1994/95 and then to those for each year between 2007/08 and 2013/14.

For the year-effect growth model, \( t_1 \) and \( t_n \) denote the first and last years of sampling, respectively, and \( A \) represents the maximum age at the beginning of year \( t_1 \) for the year classes of fish present in that year. Note that these fish would be \( A + n - 1 \) years old at the beginning of the last sampling period, i.e. the beginning of year \( t_n \). The model assumes that, within each year \( t \) \((t_1 \leq t \leq t_n)\), fish grow in accordance with a von Bertalanffy growth curve with year-specific growth parameters, \( L_{\infty} \) and \( k \), which represent the asymptotic length and a coefficient that determines the rate at which fish of a given length approach that asymptotic length, and \( t_0 \), the
age at which, in theory, the fish would have zero length, and is assumed to be constant for all
year classes. The model also assumes that fish do not undergo negative growth, and that the
length at age 0 years of fish within each year class \( y \), which was recruited to the population
during the sampling period, may be calculated using the von Bertalanffy growth curve and the
growth parameters for that year, i.e. for \( t = y \), and the common value of \( t_0 \). The initial lengths at
the beginning of year \( t_i \) of the fish of year classes already recruited to the population before the
first year of the sampling period, i.e. fish of ages 1 to \( A \) years, vary and are represented as the
parameters \( L_1 \) to \( L_A \).

Let \( \hat{L}_{t,y} \) represent the expected length of a fish from year class \( y \) at the start of year \( t \), where
\( t \geq y \) and where the age of the fish at that time is \( a = t - y \) years. From the above assumptions,
it follows that \( \hat{L}_{t+1,y} = \hat{L}_{t,y} \) if \( \hat{L}_{t,y} \geq L_{\infty t} \), otherwise \( \hat{L}_{t+1,y} = \hat{L}_{t,y} + (L_{\infty t} - \hat{L}_{t,y})\{1 -
\exp(-k_t)\} \). It also follows that, when captured at decimal age \( a_j \) years, the length \( \hat{L}_j \) of the \( j \)’th
fish, which was of year class \( y_j \), may be estimated as \( \hat{L}_j = \hat{L}_{[a_j+y_j],y_j} \) if \( \hat{L}_{[a_j+y_j],y_j} \geq L_{\infty[a_j+y_j]} \),
otherwise \( \hat{L}_j = \hat{L}_{[a_j+y_j],y_j} + (L_{\infty[a_j+y_j]} - \hat{L}_{[a_j+y_j],y_j})\{1 - \exp[-k_{[a_j+y_j]}(a_j - [a_j])]\} \), where
the year in which the fish is caught is calculated as \( t = [a_j + y_j] \), and where \([x]\) represents
the ‘floor’ function of \( x \), i.e. the greatest integer less than or equal to \( x \). The above equation thus
represents the expected length following a period of growth of \( a_j - [a_j + y_j] \) years from an
initial length \( \hat{L}_{[a_j+y_j],y_j} \) at the start of year \( t \), where growth is in accordance with a von
Bertalanffy growth model with the growth parameters for the year of capture, i.e. \( L_{\infty[a_j+y_j]} \) and
\( k_{[a_j+y_j]} \).

For year classes \( y = t_1 \) to \( t_2 \), \( \hat{L}_{t_2,y} = L_{\infty y} \{1 - \exp[k_y t_0]\} \), where \( t_0 \) is common. Finally,
for year classes \( y < t_1 \), \( \hat{L}_{t_1,y} = L_{t_1-y} \).

When fitting the above model, the log-likelihood \((LL)\) was calculated assuming that the
observed length at age of each fish at its date of capture was normally distributed, with common
variance, about the estimated length at age at that date. The parameters estimated when fitting
the model comprised the year-specific values of $L_{x,t}$ and $k_t$ (where $t_1 \leq t \leq t_n$), a common
value of $t_0$, and the initial lengths $L_a$ for $1 \leq a \leq A$.

For each set of lengths at age for each sex in 1993-95 and 2007-14, a traditional von
Bertalanffy growth curve, with parameters $L_\infty$, $k$ and $t_0$, was first fitted by maximizing $LL$. The
year-effect model was then fitted, using common values for $L_\infty$ and $k$ for each year and a
common $t_0$, to obtain estimates of the parameters for the initial lengths $L_a$ for $1 \leq a \leq A$. ‘All
subsets regression’ (Berk, 1978) was then used to identify the model with year-specific values of
$L_{x,t}$ and $k_t$ which, as parameters were successively added (while retaining common values for
$L_\infty$ and $k$ for the remaining years), provided the best representation of the lengths at age at each
successive level of increasing complexity, i.e. with $A + 4$, $A + 5$, …, $A + 2n + 1$ parameters.

With the addition of each parameter, the Akaike Information Criterion (AIC) of the best fitting
model at each level of complexity was compared with that of the best fitting model at the
previous level of complexity. The model with the smaller AIC value was accepted as the better
of the two models. AIC was calculated as $AIC = 2n_p - 2LL$, where $n_p$ is the number of
parameters.

The observed lengths at age of each year class within each yearly sample were resampled
(with replacement) to produce samples of the same size as in the original data for that year class.
The resampled data for the different year classes were then combined and the model fitted (as
described above) to the resultant data set. This bootstrapping process was repeated 1000 times.
The approximate 95% confidence limits for the parameters and estimated length of fish within
each year class at each age were taken as the 2.5 and 97.5 percentiles of the estimates produced
by the resampling procedure. The means of the predicted lengths were plotted against the means
of the observed lengths at age of the 2+, 3+ and 4+ age classes, which had each passed through
two or more summers of growth and were represented by substantial numbers, to demonstrate that the model provided a good representation of the data.

A simulation study was used to confirm that, for each sex in 1993-95 and 2007-14, a model of the form described above was capable of producing reliable parameter estimates when applied to data of the type recorded for *A. butcheri* in the Swan River Estuary. Thus, the model was fitted to simulated lengths at age to test whether it could recover the specified ‘true’ values of the model parameters used to generate the simulated data. Simulated lengths at age were generated for each of the observed ages at capture of the fish within each year class in each annual sample, assuming that these lengths were normally distributed about the mean lengths at age calculated using the different values of $L_\infty$ and $k$ for each year and a common standard deviation. The values of these parameters and the standard deviation of ‘observed lengths at age’ about the predicted lengths at age were those that had been determined when first fitting the year-effect model to each sex within each period. The same sample sizes for each year class within each annual sample, as in the original data set, were used when generating each simulated data set. The process was repeated for 1000 simulated data sets and the resultant parameters compared with the parameters used to generate the data. Overall percentage bias was estimated separately for $L_\infty$, $k$ and the parameters representing the initial lengths for each sex and each period as

$$\frac{\sum_{i=1}^{n_p}(100(x_{i,\text{true}} - \hat{x}_i)/x_{i,\text{true}})}{n_p}$$

where $x_{i,\text{true}}$ is the specified value for parameter $i$ and $\hat{x}_i$ is the mean of that parameter estimated for the $n = 1000$ simulated data sets. Percentage Root Mean Square Error (%RMSE) of that estimate was calculated as

$$\frac{100}{n_p}\sum_{i=1}^{n_p} \sqrt{\frac{1}{n}\sum_{j=1}^{n}(x_{i,j} - x_{i,\text{true}}/x_{i,\text{true}})^2}$$

2.4. *Inter-annual variations in growth and relationship between growth and environmental variables*

The year-specific growth parameters, derived from the year-effect model, were used to calculate annual length increments for females and males of *A. butcheri* in each year in 1993-95
and 2007-14. These length increments were calculated for fish with a TL of 115 mm, the approximate TL at the commencement of the second year of life, thus providing a standardised basis for comparing, within and between periods, the amount of annual growth that occurs during an age when considerable growth occurs.

The means of the predicted annual length increments for each year in 2007-14 were plotted against the annual means of the maximum monthly air temperatures between November and March, i.e. during the warmest part of the year when intra-annual growth mainly occurs, and against annual means of freshwater discharges in the immediately preceding months of June to September, i.e. when the vast majority of rainfall occurs. A one-tailed t-test of the Pearson correlation coefficient was used to test whether the means of the predicted annual length increments in the seven years between 2007/08 and 2013/14 were positively related to temperature, as hypothesised, and a two-tailed t-test employed to explore whether those increments were related to freshwater discharge.

3. Results

3.1. Temperature and freshwater discharge

Mean annual maximum air temperature increased progressively and in an essentially linear manner between 1990 and 2014, with the least value of 23.5°C recorded in 1990 and the greatest of 26.1°C in 2010 (Fig. 2, \( r = 0.73, P<0.001 \)). The linear equation relating temperature (\( T \)) to year (\( Y \)) was \( T = 0.07Y - 109.5 \) and thus mean annual maximum air temperature increased on average by 0.07°C y\(^{-1}\) over that period. Conversely, the mean annual freshwater discharge decreased in an exponential fashion with year (Fig. 2), as described by the log-linear equation relating freshwater discharge (\( D \)) and year, i.e. \( \ln(D) = -0.08Y + 159 (r = -0.63, P<0.001) \). Mean annual freshwater discharge ranged from 5.6 to 21.9 m\(^3\) s\(^{-1}\) between 1990 and 1999, from 2.6 to 9.4 m\(^3\) s\(^{-1}\) between 2000 and 2009 and never exceeded 4.8 m\(^3\) s\(^{-1}\) between 2010 and 2014.
3.2. Model parameter selection and simulation

The inclusion of parameters representing the initial lengths of the females and males of *A. butcheri* with ages ≥ 1 year at the start of 2007-14 resulted in better fits of the model to the lengths at age for both sexes than when using traditional von Bertalanffy growth models for that period. Thus, the inclusion of the initial length parameters led to the AIC decreasing from 37384 to 36961 for females and from 35836 to 35489 for males. The AICs for females in 2007-14 continued to decline with the addition of nine of the twelve year-specific growth parameters ($L_\infty$ and $k_s$) for those years (AIC = 36203, Tables 1, 2) and the same trend was true for males with the addition of ten of the twelve year-specific growth parameters (AIC = 34710).

As with 2007-14, the inclusion of parameters representing the initial lengths of the females and males of *A. butcheri* with ages ≥ 1 year at the start of 1993-95 improved the model fits for both sexes beyond those produced by traditional von Bertalanffy growth models (AIC = 5491 vs 5543 for females and 6059 vs 6074 for males). In contrast to 2007-14, however, the inclusion of separate year-specific $L_\infty$s and $k_s$s for females in the model did not further improve the fit in 1993-95. The inclusion of separate year-specific $k_s$s, but not $L_\infty$s (Table 2), did improve slightly, however, the fit of the model for males in 1993-95 (AIC = 6054 vs 6059).

As demonstrated by the overall absolute percentage biases and %RMSEs, the year-effect model estimated accurately the year-specific parameters and the initial length parameters for both sexes and periods (Table 3).

3.3. Model results

The lengths at age predicted by the year-effect model for females and males of *A. butcheri* in the two years in 1993-95 and seven years in 2007-14 provided a good fit to the observed lengths at age, with no conspicuous systematic deviations of those lengths from the fitted curves (Fig. 3). There were, however, discontinuities between the curves describing the lengths at age of successive age classes in each year (*i.e.* 12 month interval). These discontinuities reflect the fact
that the growth of fish of a particular age varies among years and thus fish of the same age attain different lengths in the different years. For example, for females at 4.0 years of age, the predicted mean length of 217 mm in 2010/11 was greater than the 192 mm in 2009/10 (Fig. 3). The inter-annual variations in lengths at age are reflected in differences in both of the year-specific von Bertalanffy growth parameters \( (k \text{ and } L_\infty) \) for each sex in 2007-14 (Table 1). Thus, for example with females, the mean values for \( k \) ranged from 0.14 to 1.03 y\(^{-1}\) and those for \( L_\infty \) ranged from 161 to 582 mm.

On the basis of the year-specific growth parameters and an initial length of 115 mm (the average predicted length at the commencement of the second year of life), female *A. butcheri* increased in length by 88 mm in both 1993/94 and 1994/95 (Fig. 4). These annual increments were greater than those estimated for females in each of the seven years in 2007-14. The trends exhibited by the annual length increments by males followed a very similar pattern, with the annual increment of 63 mm in 1993/94 and 82 mm in 1994/95 being greater than in each year between 2007-14, apart from 2010/11 in which, even then, the maximum value was virtually the same as in 1994/95 (Fig. 4). During the 2007-14 period, the maximum and minimum annual length increments of both sexes differed by a factor of ~2.

**3.4. Relationship between growth and temperature and freshwater discharge**

The predicted annual length increments of 1+ *A. butcheri* in the years between 2007/08 and 2013/14, based on an initial length of 115 mm, were positively correlated with the mean maximum air temperature in November to March in the case of both females (Fig. 5, \( r = 0.68, P<0.05 \)) and males (Fig. 5, \( r = 0.77, P<0.05 \)). The same annual length increments were not significantly correlated with freshwater discharge in the preceding months of June to September, *i.e.* when the vast majority of rainfall occurs, in the case of either females (Fig. 5, \( r = 0.26, P>0.05 \)) or males (Fig. 5, \( r = -0.01, P>0.05 \)).
3.5. Trends exhibited by observed lengths at age between 1993 and 2014

The means of the observed lengths for the females and males of the 2+, 3+ and 4+ age classes of *A. butcheri* in the intervening years between 1993-95 and 2007-14 (for which the data were obtained using a slightly different sampling regime and thus not included in the year-effect model) declined in a manner consistent with the trends exhibited by the means of the observed (and predicted) lengths of those age classes in the preceding and subsequent years (Fig. 6). The mean observed lengths for each age class followed a smooth trend over the 21 years of sampling. Thus, the means of the observed lengths for both sexes declined progressively from 1993/94 to ~2007/08 and then rose until ~2011/12, before declining again in 2013/14. For example, with 3 year old females, the means of the observed lengths decreased from 288 mm in 1993/94 to 178 mm in 2007/08 and then rose to 218 mm in 2011/12 before falling to 190 mm in 2013/14 (Fig. 6).

4. Discussion

4.1. Value of using a year-effect model and length-at-age data

The year-effect model, developed for this study, provided a more comprehensive description of the somatic growth of female and male *Acanthopagrus butcheri* in the Swan River Estuary in the two years in 1993-95 and seven years in 2007-14 than that produced by the traditional von Bertalanffy growth model. The production of reliable year-specific growth parameters thus enabled us to determine the extent to which the somatic growth of *A. butcheri* varied annually and whether the growth of both of its sexes in each year in the latter period was consistently less than in the former period. In addition, the annual length increments produced by the model allowed us to test whether the growth of *A. butcheri* in the years in the 2007-14 period was related to temperature and freshwater discharge. Our modelling approach also permitted us to follow Szalai *et al.* (2003) and He & Bence (2007) in elucidating whether growth was influenced...
by such factors, without specifying the precise functional relationships required for their inclusion as covariates in the growth model.

The application of a year-effect model to length-at-age data to quantify inter-annual variations in growth parameters and thereby estimate the annual increments in the length of young (1+ age class) *A. butcheri* in the Swan River Estuary, after standardising for initial length, differs from approaches typically used in otolith-based studies of inter-annual growth. Thus, in those other studies, variations in the widths of the growth zones in otoliths to develop chronologies for the relative growth of otoliths in different years and in mixed-effect models to determine *inter alia* the influence of age and year on otolith growth (e.g. Weisberg *et al.*, 2010; Morrongiello *et al.*, 2012; Coulson *et al.*, 2014). Otolith-based approaches have been employed in studies of *A. butcheri* in estuaries further east in Tasmania and South Australia (Doubleday *et al.*, 2015) and of another estuarine species, *P. colonorum*, in Victoria (Morrongiello *et al.*, 2014).

Length-based and otolith-based approaches enable estimates to be made of inter-annual variations in the growth of the body and otolith, respectively, and thereby allow the relationship of that growth with environmental variables to be explored. Length-based approaches have the advantage of providing a direct and readily interpretable measure of annual change in body size, whereas otolith-based approaches have the advantage of yielding data on growth in the years prior to sampling. While otolith-based approaches assume that annual increments in length are directly proportional to those in the otolith, such a relationship is not always the case with, for example, otoliths typically continuing to grow after the growth in the body has slowed markedly or even ceased (e.g. Campana, 1990; Morrongiello *et al.*, 2012). At the same time, however, it is likely that, in terms of body length, any relationship between growth and an environmental variable will be mirrored by a similar trend with otolith growth (Morales-Nin, 2000).

4.2. *Inter-annual variations in growth*
The year-effect model demonstrated that the growth of both sexes of *A. butcheri* in the Swan River Estuary varied markedly among years in 2007-14, the period for which there were length-at-age data for a number of sequential years. These inter-annual differences are reflected in discontinuities in the growth trajectories, derived from the year-effect model, for sequential age classes in each of these years (Fig. 3). They are also reflected in marked differences among the mean annual length increments predicted by the year-effect model for fish with an initial TL of 115 mm, which corresponds approximately to the length at the beginning of the second year of life. These mean annual length increments, which represent standardised estimates of the amount of growth undergone during the year by one year old fish, varied by a factor of ~2 in the years between 2007/08 and 2013/14. When comparisons were extended to include the two years in the earlier period, *i.e.* 1993/94 and 1994/95, the extent of the inter-annual differences in length increments of females and males across all of the nine years, for which data were analysed using the model, increased to ~2.5. In terms of body mass, the differences in the corresponding maximum and minimum mean increments of both sexes, derived from the length-weight relationship for *A. butcheri* in the Swan River Estuary (Cottingham *et al.*, 2014), increased to ~2.7 times for the seven years between 2007/08 and 2013/14 and to ~5 times across the nine years for which the data were modelled. These marked inter-annual differences in growth reflect the plasticity of the biological characteristics of *A. butcheri* and the ability of this species to respond to changes in environmental conditions. This type of plasticity, which is typical of sparids, is also reflected in the marked differences between the biological characteristics of such species in different water bodies in the southern hemisphere (*e.g.* Sarre & Potter, 2000; Griffiths *et al.*, 2002; Partridge *et al.*, 2004; Chuwen *et al.*, 2007; Sim-Smith *et al.*, 2012; Wakefield *et al.*, 2015).

It is highly relevant that the mean annual length increments, estimated by the model for females and males in the Swan River Estuary in each year between 2007/08 and 2013/14, were
less than those for the corresponding sex in 1993/94 and 1994/95 in all cases except for males in 1993/94 and, even then, the value was essentially the same as the maximum recorded for males in 2007-14. The above marked differences emphasise that, even when the pronounced inter-annual variations in growth of *A. butcheri* are taken into account, growth was almost invariably less in the recent than earlier period. These trends account for the previous finding that, overall, the growth of *A. butcheri* in the Swan River Estuary declined between 1993-95 and 2007-11 (Cottingham *et al.*, 2014).

In the context of inter-annual variations in growth in 2007-14, it is relevant that the annual length increments of the females and males of *A. butcheri*, during their second year of life, when appreciable growth is still occurring, were both positively related to temperature, which is consistent with the trends exhibited by many fish species (Angilletta *et al.*, 2010; Neuheimer *et al.*, 2011). This finding also parallels the results of Doubleday *et al.* (2015) and Morrongiello *et al.* (2014) using otoliths, which demonstrated that the growth of the otoliths of *A. butcheri* and *P. colonorum* in estuaries further east in mainland Australia was related to temperature, with this variable the most influential of those analysed in the second of those studies. In contrast, the growth of otoliths of *A. butcheri* in Tasmania exhibited a weak negative correlation with temperature (Doubleday *et al.*, 2015).

Freshwater discharge has often been regarded as important in influencing the growth of fish species in estuaries, through, for example, supplying nutrients that promote primary and thus secondary productivity (Darnaude *et al.*, 2004; Robins *et al.*, 2006; Purtlebaugh & Allen, 2010). The present study demonstrated, however, that, during 2007-14, the annual length increments of one year old *A. butcheri* in the Swan River Estuary were not significantly correlated with freshwater discharge in June to September, when the vast majority of discharge occurs. It is therefore relevant that discharge very largely occurs prior to the spawning period and main growth phase of *A. butcheri* and that, in contrast to its pronounced downward trend between the
early 1990s and mid-2000s, such discharge had largely levelled off during subsequent years (Fig. 2). Although Doubleday et al. (2015) found that the growth of *A. butcheri* was poorly related to freshwater discharge in the Murray River Estuary, they point out that this system is subjected to water abstraction and regulation. While Morrongiello et al. (2014) found that the growth of the otoliths of *P. colonorum* was related to freshwater discharge, this influence was less than that of temperature.

4.3. Trends in growth over two decades

The trends in the growth of the 2+, 3+ and 4+ age classes of *A. butcheri* in the Swan River Estuary between 1993 and 2014, determined by analyses undertaken in the present study, can now be considered in the context of changes in the environmental conditions of this system over two decades. In contrast to the annual length increments, derived from the model for one year old fish in a given year and employed in discussions in preceding sections, the mean observed lengths of the 2+, 3+ and 4+ age classes in a given year represent the cumulative growth over the preceding two, three and four years, respectively. They thus represent the ‘average’ growth over life of those age classes over those years, rather than the growth of a particular age class in a given year.

The clear and consistent trends exhibited by the means of the observed lengths of the above three age classes emphasise that the growth of *A. butcheri* in the Swan River Estuary declined progressively between the early 1990s and mid-2000s. The data in Cottingham et al. (2014) provided strong circumstantial evidence that the differences between the overall growth of *A. butcheri* in the 2007-11 and 1993-95 periods was related to the effects of increased hypoxia in deeper waters and consequently also to habitat compression of this species into shallow waters, thereby resulting in an increase in density in those waters. The increase in hypoxia was due to an increased accumulation of nutrients and organic materials in deeper waters as a result of
reductions in rainfall and therefore of freshwater discharge and its flushing effect. The estuaries of south-western Australia are particularly prone to the deleterious effects of such accumulations because they have long residence times, as a result of their location in a microtidal region and where little rainfall and thus freshwater discharge occur during the warmer months of the year (Tweedley et al., 2012, 2014).

As temperature increased markedly between the early 1990s and mid-2000s, the decline in growth that occurred in the intervening period runs counter to the relationship recorded between growth and temperature for many fish species and is not consistent with the metabolic theory of ecology (Brown et al., 2004; Weber et al., 2015). Thus, any potential positive relationship between growth and temperature was over-ridden by hypoxia and related effects, such as increased density (see above). However, even though data on subsequent growth and temperature were available for modelling for only seven years, i.e. those between 2007/08 and 2013/14, the length increments for females and males, during essentially the second year of life of A. butcheri, were, as discussed above, positively correlated with temperature. It is thus relevant that, by this period, the majority of fish were congregated in the shallow waters and their densities were not undergoing a conspicuous increase or decrease.

As A. butcheri is typically confined to its natal estuary for the whole of its life cycle (Chaplin et al., 1998; Burridge & Versace, 2006; Cottingham et al., 2014), the individuals of this species are exposed, throughout life, to any deleterious changes in environmental quality within that estuary. This feature, allied with its plastic biological characteristics, makes A. butcheri an ideal candidate for exploring the ways and extent to which certain key biological characteristics of a fish species respond to detrimental and other changes in its environment. Consequently, as with the Spotted Sea Trout C. nebulosus in estuaries in North America (Bortone, 2003; Bortone et al., 2006), A. butcheri has the potential to act as a valuable indicator of the health of an estuary and for hypothesising on the effects of climate change.
Acknowledgements

Gratitude is expressed to Gavin Sarre and Steeg Hoeksema for data for Acanthopagrus butcheri in earlier periods and to many colleagues and friends who helped with sampling, in particular, Amanda Buckland, Chris Hallett, Joel Williams, Dan Yeoh and Eloïse Ashworth. Financial and other support was provided by Recfishwest, Swan River Trust, Department of Water, Department of Fisheries and Murdoch University. This study was undertaken while the senior author was a recipient of an Australian Postgraduate Award and was conducted in accordance with conditions in permits R2278-09 and R2561/13 issued by the Murdoch University Animal Ethics Committee.

References


List of figures
Figure 1. Map showing sites at which *Acanthopagrus butcheri* was sampled in the upper Swan River Estuary. Arrow in inset map shows the location of the Swan River Estuary in Western Australia. Closed circles denote the sites sampled by seine and gill nets.

Figure 2. Mean annual maximum air temperature, recorded at Perth Airport in the vicinity of the Swan River Estuary (Australian Bureau of Meteorology, 2015), and mean annual freshwater discharge, recorded at gauging station 616011 upstream of the study area (Western Australian Department of Water, 2015). The fitted equations are also displayed.

Figure 3. Lengths at age of females and males of *Acanthopagrus butcheri* caught in the Swan River Estuary in the two years in 1993-95 and four years in 2007-11 and the lengths at age predicted by the fitted year-effect growth model.

Figure 4. Mean values (and 95% confidence intervals) for predicted annual increases in the lengths of one year old females and males of *Acanthopagrus butcheri* during each year in the 1993-95 and 2007-14 periods, using a common starting length of 115 mm, the mean length at the commencement of the second year of life.

Figure 5. Relationship between annual length increments for females and males of *A. butcheri* and (a, b) mean air temperatures and (c, d) mean freshwater discharge. Linear equations relating annual length increments to temperature are shown.

Figure 6. Mean lengths at age of female and male *Acanthopagrus butcheri* (and 95% confidence intervals) for sequential age classes in each year in the 1993-95 and 2007-14 periods, as
predicted by the year-effect growth models (closed circles) and for the observed lengths at age at
capture (open circles). Mean observed lengths at age (and 95% confidence intervals) for the
smaller samples of fish collected in 2003/04, 2004/05, 2005/06 and 2006/07 are also shown.
Table 1. Year-specific von Bertalanffy growth parameter estimates, derived by fitting a year-effect growth model to the lengths at age of female and male *Acanthopagrus butcheri* caught in the Swan River Estuary in 2007-14 and 1993-95. Approximate lower and upper 95% confidence limits were derived by bootstrapping. Italics are used to designate parameters that remained common among years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Females</th>
<th></th>
<th></th>
<th></th>
<th>Males</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$k$ (year$^{-1}$)</td>
<td>$L_\infty$ (mm)</td>
<td>$t_0$ (y)</td>
<td></td>
<td>$k$ (year$^{-1}$)</td>
<td>$L_\infty$ (mm)</td>
</tr>
<tr>
<td>2007/08</td>
<td>Average</td>
<td>0.32</td>
<td>318</td>
<td>-0.43</td>
<td>0.34</td>
<td>301</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.29</td>
<td>271</td>
<td>-0.39</td>
<td>0.25</td>
<td>273</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.37</td>
<td>340</td>
<td>-0.47</td>
<td>0.36</td>
<td>332</td>
<td>-0.42</td>
</tr>
<tr>
<td>2008/09</td>
<td>Average</td>
<td>0.52</td>
<td>192</td>
<td>-0.43</td>
<td>0.51</td>
<td>193</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.36</td>
<td>187</td>
<td>-0.39</td>
<td>0.38</td>
<td>187</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.55</td>
<td>243</td>
<td>-0.47</td>
<td>0.54</td>
<td>236</td>
<td>-0.42</td>
</tr>
<tr>
<td>2009/10</td>
<td>Average</td>
<td>0.14</td>
<td>582</td>
<td>-0.43</td>
<td>0.20</td>
<td>417</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.11</td>
<td>413</td>
<td>-0.39</td>
<td>0.16</td>
<td>338</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.21</td>
<td>717</td>
<td>-0.47</td>
<td>0.26</td>
<td>509</td>
<td>-0.42</td>
</tr>
<tr>
<td>2010/11</td>
<td>Average</td>
<td>0.43</td>
<td>282</td>
<td>-0.43</td>
<td>0.34</td>
<td>340</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.29</td>
<td>252</td>
<td>-0.39</td>
<td>0.25</td>
<td>324</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.51</td>
<td>379</td>
<td>-0.47</td>
<td>0.36</td>
<td>423</td>
<td>-0.42</td>
</tr>
<tr>
<td>2011/12</td>
<td>Average</td>
<td>0.32</td>
<td>318</td>
<td>-0.43</td>
<td>0.57</td>
<td>236</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.29</td>
<td>271</td>
<td>-0.39</td>
<td>0.45</td>
<td>192</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.37</td>
<td>340</td>
<td>-0.47</td>
<td>0.98</td>
<td>258</td>
<td>-0.42</td>
</tr>
<tr>
<td>2012/13</td>
<td>Average</td>
<td>1.03</td>
<td>161</td>
<td>-0.43</td>
<td>0.98</td>
<td>165</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.75</td>
<td>117</td>
<td>-0.39</td>
<td>0.77</td>
<td>122</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>3.68</td>
<td>187</td>
<td>-0.47</td>
<td>2.47</td>
<td>179</td>
<td>-0.42</td>
</tr>
<tr>
<td>2013/14</td>
<td>Average</td>
<td>0.32</td>
<td>280</td>
<td>-0.43</td>
<td>0.34</td>
<td>269</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.29</td>
<td>249</td>
<td>-0.39</td>
<td>0.25</td>
<td>258</td>
<td>-0.52</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.37</td>
<td>308</td>
<td>-0.47</td>
<td>0.36</td>
<td>329</td>
<td>-0.42</td>
</tr>
<tr>
<td>1993/94</td>
<td>Average</td>
<td>0.42</td>
<td>373</td>
<td>-0.14</td>
<td>0.20</td>
<td>451</td>
<td>-0.54</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.35</td>
<td>352</td>
<td>-0.24</td>
<td>0.14</td>
<td>399</td>
<td>-0.78</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.49</td>
<td>403</td>
<td>-0.06</td>
<td>0.26</td>
<td>546</td>
<td>-0.36</td>
</tr>
<tr>
<td>1994/95</td>
<td>Average</td>
<td>0.42</td>
<td>373</td>
<td>-0.14</td>
<td>0.32</td>
<td>451</td>
<td>-0.54</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.35</td>
<td>352</td>
<td>-0.24</td>
<td>0.20</td>
<td>399</td>
<td>-0.78</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>0.49</td>
<td>403</td>
<td>-0.06</td>
<td>0.42</td>
<td>546</td>
<td>-0.36</td>
</tr>
</tbody>
</table>
Table 2. Parameters representing the initial lengths ($L_a$) of female and male *Acanthopagrus butcheri* with ages $\geq 1$ year at the start of 2007-14 and 1993-95.

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>2007-14</th>
<th>1993-95</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females (mm)</td>
<td>Males (mm)</td>
</tr>
<tr>
<td>1</td>
<td>106</td>
<td>105</td>
</tr>
<tr>
<td>2</td>
<td>135</td>
<td>132</td>
</tr>
<tr>
<td>3</td>
<td>165</td>
<td>163</td>
</tr>
<tr>
<td>4</td>
<td>205</td>
<td>190</td>
</tr>
<tr>
<td>5</td>
<td>246</td>
<td>214</td>
</tr>
<tr>
<td>6</td>
<td>274</td>
<td>235</td>
</tr>
<tr>
<td>7</td>
<td>311</td>
<td>288</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Overall percentage bias and percentage root mean squared error (%RMSE) in model estimates of the year-effect parameters $L_\infty$ and $k$ and initial length parameters ($L_a$) at the start of each sampling period for female and male *Acanthopagrus butcheri* $\geq 1$ year in the Swan River Estuary in 1993-95 and 2007-14.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_\infty$2007-14 (mm)</td>
<td>-1.58</td>
<td>1.21</td>
</tr>
<tr>
<td>$k_{2007-14}$ (y$^{-1}$)</td>
<td>2.91</td>
<td>-3.39</td>
</tr>
<tr>
<td>$L_\infty$1993-95 (mm)</td>
<td>-0.30</td>
<td>-1.15</td>
</tr>
<tr>
<td>$k_{1993-95}$ (y$^{-1}$)</td>
<td>-0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>Length parameters$_{2007-14}$ (mm)</td>
<td>0.14</td>
<td>-0.03</td>
</tr>
<tr>
<td>Length parameters$_{1993-95}$ (mm)</td>
<td>0.12</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Canning River

115°50'E

Kms

0                  2.5                  5

115°E

125°E

35°S

25°S

15°S

Western
Australia

Indian Ocean

32°S

Upper Swan River Estuary

Perth

Canning River
<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>22</td>
<td>1990</td>
</tr>
<tr>
<td>24</td>
<td>1995</td>
</tr>
<tr>
<td>26</td>
<td>2000</td>
</tr>
<tr>
<td>28</td>
<td>2005</td>
</tr>
<tr>
<td>22</td>
<td>2010</td>
</tr>
<tr>
<td>24</td>
<td>2015</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Discharge (m³/s)</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1990</td>
</tr>
<tr>
<td>5</td>
<td>1995</td>
</tr>
<tr>
<td>10</td>
<td>2000</td>
</tr>
<tr>
<td>15</td>
<td>2005</td>
</tr>
<tr>
<td>20</td>
<td>2010</td>
</tr>
<tr>
<td>25</td>
<td>2015</td>
</tr>
</tbody>
</table>

![Graph showing temperature and discharge over years.](image-url)
Males

Temperature (°C)

Length increment (mm)

Females

Discharge (m³ s⁻¹)

a)

b)

c)

d)
A series of line graphs show the total length (mm) of females and males across different age classes and years. The graphs are labeled for 2+ age class, 3+ age class, and 4+ age class for both males and females. The years range from 1993/94 to 2013/14.

- **Females**:
  - 2+ age class: $n=751$
  - 3+ age class: $n=550$
  - 4+ age class: $n=384$

- **Males**:
  - 2+ age class: $n=927$
  - 3+ age class: $n=826$
  - 4+ age class: $n=503$
Highlights