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Marked deleterious changes in the condition, growth and maturity schedules of *Acanthopagrus butcheri* (Sparidae) in an estuary reflect environmental degradation

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**Abstract**

As *Acanthopagrus butcheri* typically completes its life within its natal estuary and possesses plastic biological characteristics, it provides an excellent model for exploring the ways and extent to which a fish species can respond to environmental changes over time. The environment of the Swan River Estuary in south-western Australia has deteriorated markedly during the last two decades, reflecting the effects of increasing eutrophication and hypoxia in the upper regions, where *A. butcheri* spends most of the year and spawns. In this study, the biological characteristics of *A. butcheri* in 2007–11 were determined and compared with those in 1993–95. Between these two periods, the condition factor for females and males of *A. butcheri* across their length ranges declined by 6 and 5%, respectively, and the parameters $k$ and $L_{\infty}$ in the von Bertalanffy growth curves of both sexes underwent marked reductions. The predicted lengths of females and males at all ages $\geq 1$ year were less in 2007–11 than in 1993–95 and by over 30% less at ages 3 and 6. The ogives relating maturity to length and age typically differed between 1993–94 and 2007–10. The $L_{50}$ of 161 mm for females and 150 mm for males in 2007–10 were less than the corresponding values of 181 and 170 mm in 1993–94, whereas the $A_g$ of 2.3 years for females and 2.2 years for males in 2007–10 were greater than the corresponding values of 1.6 and 1.1 years in 1993–94. The above trends in condition, growth and maturity parameters between periods are consistent with hypotheses regarding the effects of increasing hypoxia on *A. butcheri* in offshore, deeper waters. However, as the density of *A. butcheri* declined in offshore, deeper waters and increased markedly in nearshore, shallow waters, density-dependent effects in the latter waters, although better oxygenated, also probably contributed to the overall reductions in growth and thus to the changes in the lengths and ages at maturity.

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1. Introduction

Estuaries are among the most productive of all aquatic ecosystems (Schelske and Odum, 1961; Whittaker and Likens, 1975; Elliott and Whitfield, 2011), which helps account for their importance as a nursery area for many marine fish species throughout the world (Blaber and Blaber, 1980; Potter et al., 1990; McLusky and Elliott, 2004; Able and Fahay, 2010). This rich food source is also crucial for those species that complete their life cycles within estuaries and which are particularly abundant in temperate microtidal regions of the southern hemisphere, such as those of south-western Australia (Potter and Hyndes, 1999; Whitfield, 1999; Chuwen et al., 2011).

Despite their ecological significance, estuaries are also among the most degraded of all marine ecosystems (Jackson et al., 2001), with the prevalence of those systems that have become eutrophic due to anthropogenic impacts increasing markedly during recent...
decades (Kennish and Townsend, 2007; Vaquer-Sunyer and Duarte, 2008). Furthermore, eutrophication in estuaries that experience strong vertical stratification enhances the rate of accumulation of organic matter and thus ultimately leads to hypoxia in their deeper waters (Diaz, 2000; Eby et al., 2005; Breitburg et al., 2009). Hypoxic conditions can be lethal to fish and have a detrimental effect on their early development (Wannamaker and Rice, 2000; Thronson and Quigg, 2008; Hassell et al., 2008a, b) and lead to reductions in their body condition, growth rates and metabolism (Pichavant et al., 2000, 2001; Wu, 2002; Eby et al., 2005). While fish sometimes have the opportunity to move from hypoxic to better oxygenated habitats (Pihl et al., 1992; Howell and Simpson, 1994; Thiel et al., 1995), such as from deeper to nearshore, shallow waters in estuaries, this can lead to density-dependent effects on growth (Eby and Crowder, 2002; Campbell and Rice, 2014) and/or exposure to suboptimal temperatures and salinities (Kramer, 1987; Craig et al., 2001; Eby et al., 2005).

Most studies of the ways in which reductions in growth are reflected in changes in the maturity schedules of fish populations have been undertaken on populations subjected to substantial fishing pressure (e.g. Morita and Fukuwaka, 2007; Stahl and Kruse, 2008). In many cases, such reductions in growth were accompanied by a decline in the length at maturity (Morita and Morita, 2002; Morita and Fukuwaka, 2007) and an increase in the age at maturity, which is consistent with, for example, the model of Stearns (1992) in which such trends represented a balance between reducing fecundity and increasing mortality. Certain studies support this model (Helle and Hoffman, 1998; Morita and Morita, 2002; Grover, 2005; Morita and Fukuwaka, 2007), but none has determined quantitatively, and in a composite manner, the declines in the growth of a species in an estuary as that system became degraded and the reductions in body condition and changes in maturation schedules that accompanied that deterioration.

The large microtidal Swan River Estuary, which runs through the city of Perth on the lower west coast of Australia, discharges into the Indian Ocean. During the last 20 years, this permanently-open microtidal estuary, and particularly its riverine upper reaches, has become increasingly eutrophic (Stephens and Imberger, 1996; Hamilton and Turner, 2001; Thomson et al., 2001; Robson and Hamilton, 2003). Thus, while phytoplankton blooms were rarely observed in the 1980s (Zammit et al., 2005), they occurred intermittently in the 1990s (Viney and Sivapalan, 2001) and in most years in the 2000s (Robson and Hamilton, 2003; Hallengaef et al., 2010; Kristiana et al., 2012). Indeed, this system was one of the two most hypertrophic of the 131 estuarine coastal ecosystems worldwide for which data were recently collated by Cloern et al. (2013). The upper reaches of the Swan River Estuary often experience strong stratification during the warm summer months, when freshwater discharge is typically limited and the salt wedge penetrates rapidly along the bottom of the estuary. As the deeper waters are poorly flushed, i.e. have a long residence time, and contain substantial amounts of organic material, the biological oxygen demand leads to reductions in oxygen concentrations in those waters (Norlem et al., 2014; Tweedley et al., 2014). This problem has become exacerbated over the last three decades by a decline in freshwater discharge (Western Australian Department of Water, 2014), resulting from reduced rainfall (Australian Bureau of Meteorology, 2014), and a greater penetration of the salt wedge upstream. This has led to elevated nutrient concentrations (Robson et al., 2008) and a greater prevalence of prolific algal blooms (Tweedley et al., 2014) and toxic fish species such as the black bream Acanthopagrus butcheri (Smith, 2006; Kristiana et al., 2012).

Acanthopagrus butcheri, which attains a total length of ca 530 mm and a body mass of 3450 g (Hutchins and Thompson, 2001), is abundant in many estuaries in southern Australia (Hutchins and Thompson, 2001; Gomon et al., 2008). Although A. butcheri is mobile and can swim several kilometres in a day (Hindell et al., 2008; Sakabe and Lyle, 2010), it tends to reside, for much of the year, in the upper reaches of estuaries, where it spawns during spring and early summer (Saar and Potter, 2000; Nicholson et al., 2008; Williams et al., 2012). This sparid can be swept out of the estuary during particularly heavy freshwater discharge and, in south-eastern Australia, may occasionally enter other estuaries (Lenanton et al., 1999; Burridge and Versace, 2006). These results of studies of the reproductive biology and distribution of the various life cycle stages of this species in south-western Australian estuaries imply that the individuals of this sparid complete their life cycle within their natal estuary in this region (Potter and Hynes, 1999; Saar and Potter, 2000; Williams et al., 2013). Such a conclusion is consistent with the fact that the genetic compositions of A. butcheri in the various estuaries of south-western are significantly different (Chaplin et al., 1998), noting that this also applies to those in south-eastern Australia (Burridge and Versace, 2006).

As with other sparids, the biological characteristics of Acanthopagrus butcheri are strongly influenced by the different environmental characteristics. For example, among four south-western Australian estuaries, the total lengths reached after three years ranged widely from 146 to 266 mm (Saar and Potter, 2000) and the L50s and A50s for maturity for females ranged markedly from 157 to 218 mm and 1.9–4.3 years, respectively. It is also evident, however, that maturity tends to occur at a smaller size and older age in those estuaries in which growth is less rapid (Saar and Potter, 1999, 2000), which is consistent with the model of Stearns (1992).

The present study has determined the biological characteristics of Acanthopagrus butcheri in the Swan River Estuary in 2007–11 and compared these with those derived from data collected in 1993–95 (Saar and Potter, 1999, 2000). These comparisons were used to test the hypothesis that increased environmental degradation in this estuary during recent years has been accompanied by a decline in the condition, growth and length at maturity of A. butcheri and an increase in its age at maturity. The trends exhibited by the catch data derived from fishery-independent sampling over time were compared to determine whether there was evidence that an increase in the extent of hypoxia in deeper waters had been accompanied by a reduction in the relative abundance of A. butcheri in those waters and a resultant increase in nearshore, shallow waters.

2. Materials and methods

2.1. Physico-chemical data and sampling regimes

Measurements of freshwater discharge, entering the Swan River Estuary at gauging station 616011 upstream of the study area, were provided by the Western Australian Department of Water. That department also provided weekly vertical profiles of oxygen concentration, temperature and salinity, recorded since 1995 using a YSI sonde (model 6600V2) or equivalent, at five of its sampling stations (KIN, MAY, RON, STJ, SUC) that are located within the study area. The average oxygen concentration in the bottom 1 m of the water column at each station was calculated for each weekly sample up to and including those in 2010, the last year for which data have thus far been collated. Linear interpolation between stations was then used to determine the average weekly oxygen concentrations along the central channel of the upper estuary for each year. Estimates <4 mg/L are regarded as hypoxic. The

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percentages of the total distance along the channel that was hypoxic in each week were then determined and used to calculate each annual mean.

*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 winter 2007 and autumn 2011, and thus seasonally in four consecutive 12 month intervals (Appendix). 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 winter 2007 and autumn 2009 (i.e. seasonally over two consecutive 12 month intervals), after which it was discontinued as it was catching few fish. The data on condition and growth of *A. butcheri* caught by the seine and gill netting are subsequently regarded as representing the 2007–11 period.

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 m², 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 m². 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 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 2–6 m and retrieved 3 h later.

The study of *Acanthopagrus butcheri* in 1993–95, used for comparison with the current study, was undertaken between winter 1993 and autumn 1995 (Sarre and Potter, 2000) and thus covered two consecutive 12 month intervals, subsequently referred to collectively as the 1993–95 period in descriptions of condition and growth. In that earlier study, a 41.5 m seine net (with the same dimensions as given above) was used to sample six sites, which corresponded to six of the nine seine net sites subsequently employed in 2007–11, and a gill net (with the same dimensions and mesh sizes as given above) to sample the same nine sites as later sampled by a gill net in 2007–09 (Appendix, Fig. 1).

Comparisons were also made with the data from a subsample of *Acanthopagrus butcheri* collected in each season between spring 2003 and winter 2004 using seine nets (21.5 m and 41.5 m) and a gill net at the same six and nine sites, respectively, as in 1993–95 (S. Hoeksema, unpublished data). Each net had the same dimensions and mesh sizes as in the other studies. This 12 month interval is subsequently referred to as the 2003–04 period (Appendix).

Catches of *Acanthopagrus butcheri* during the summer, winter and spring of 2000, which were obtained as part of another study that involved gill netting at the same nine sites as in 1993–95 and 2007–11 (Appendix), were used to provide catch per unit effort data for 2000 (S. Hoeksema, unpublished data).

All fish were anaesthetised in an ice slurry immediately after capture.

### 2.2. Assessment of body condition

As in previous studies, each *Acanthopagrus butcheri* caught in the upper Swan River Estuary in 2007–11 was measured to the nearest 1 mm (total length), weighed to the nearest 1 g and its sex determined by macroscopic examination of its gonads (Sarre and Potter, 2000). The smallest fish, which could not be sexed, were designated randomly (and in equal numbers) as females and males. The sagittal otoliths and gonads of each *A. butcheri* were removed and the latter weighed to 0.01 g.

Following the approach of Froese (2006), the length–weight relationships of each sex in 2007–11 and 1993–95 were calculated from data for ten randomly-selected fish from each of three length categories, i.e. <160, 180–220, >240 mm, in each calendar season, except for winter in which ten fish were not always available for each of these length categories due to the pronounced tendency for *Acanthopagrus butcheri* to be flushed downstream in that season when freshwater discharge is far greater than in other seasons (Sarre and Potter, 1999). The parameters $a_{period}$ and $b_{period}$ of the length–weight relationships, $W = a_{period} L^{b_{period}}$, were estimated by fitting linear equations of the form: $\ln(W_j) = \ln(a_{period}) + b_{period} \ln(L_j) + \epsilon_{period,j}$, to the masses (g) and

![Fig. 1. Map showing sites (closed circles) at which Acanthopagrus butcheri was sampled by seine and gill nets in the upper Swan River Estuary. Arrow in insert map shows the location of the Swan River Estuary in Western Australia.](image-url)
demonstrated that the counts of opaque zones on whole otoliths of males of *Acanthopagrus butcheri* in 2007–11 and, to facilitate direct statistical comparisons, the VBGM was refitted to the lengths at age of each sex recorded in 1993–95. The von Bertalanffy growth equation is \( L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \), where \( L_t \) is the expected total length at age \( t \) (years), \( L_\infty \) is the asymptotic length (mm), \( k \) is the growth coefficient (year\(^{-1}\)) and \( t_0 \) is the hypothetical age (years) at which fish would have zero length.

The growth curves of female and male *Acanthopagrus butcheri* in 2007–11 were compared with those of the corresponding sexes in 1993–95 using a likelihood-ratio test (see Cerrato, 1990). As the test demonstrated that the growth curves differed between these periods (see Results), likelihood-ratio tests were also conducted to determine which of the growth parameters likewise differed.

The above procedures were also used to fit the growth curves to the more restricted data for females and males in 2003–04 and to compare these and their parameters with those for 1993–95 and 2007–11.

2.4. Reproductive biology

The gonads of each female and male of *Acanthopagrus butcheri*, caught during the spawning periods in 2007–2010 and in 1993 and 1994, were examined macroscopically and allocated to one of the following maturity stages described by Sarre and Potter (1999), i.e. I = immature, II = virgin/maturing virgin, III = developing, IV = maturing, V = prespawning, VI = spawning, VII = spent and VIII = recovering spent.

Logistic regression analysis was used to determine the probability \( P \) that a female or male of a given length possessed gonads at stages III–VIII in November, i.e. just after the mid-point of the spawning period in October, when no immature fish would be expected to become mature during the current spawning season and would have included all fish that had spawned or were destined to spawn in a given spawning season. This procedure used data derived from samples collected in the Novembers of 1993 and 1994, collectively, and the Novembers in each year between 2007 and 2010, collectively. The logistic equation is

\[
\log\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1 L
\]

where \( \beta_0 \) and \( \beta_1 \) are the intercept (but not both) remained constant, and that latter model was calculated as

\[
\text{sex} = \frac{\text{mass}}{\text{length}}
\]

To compare, for each sex, the model that assumed a common weight–length relationship for that period (Tesch, 1968). A model was fitted separately to the lengths at age of females and males of *Acanthopagrus butcheri* in 2007–11 and, to facilitate direct statistical comparisons, the VBGM was refitted to the lengths at age of each sex recorded in 1993–95. The von Bertalanffy growth equation is

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lengths. The prior distribution for each parameter was represented by a non-informative normal distribution.

The above approach was also used to relate the probability that a female or male possessed mature gonads to the age of the fish and to test whether, for each sex, the ogives relating maturity to age in 1993–94 and 2007–10 were different and, if so, whether this could be attributed to a difference in the values of $A_0$. OpenBUGS was again employed, but with 2,004,000 iterations of two chains, a burn-in of 4000 and thinning interval of 40.

2.5. Measures of relative abundance

The numbers of Acanthopagrus butcheri caught on each sampling occasion in each season except winter (see below for rationale), using the 41.5 m seine net at six sites in nearshore, shallow waters of the upper estuary in different years (Appendix), were converted to a density (fish 100 m$^{-2}$). The numbers of fish caught using the multi-mesh gill net at nine sites in offshore, deeper waters of the upper estuary on each sampling occasion were expressed as number of fish gill net$^{-1}$. Although A. butcheri typically occupies the lower and saline regions of the tributary rivers, which constitute the upper estuary, many individuals are flushed downstream during winter when freshwater discharge increases sharply (Sarre and Potter, 1999). The data for this study were thus not included in analyses of the densities and catch rates. Note also that, except in 2000, the mean densities and catch rates and 95% confidence interval for a ‘year’ were calculated using consecutive seasonal data for the spring in one year and summer and autumn of the following year and thus encompass seasons in two consecutive calendar years (Appendix).

Prior to subjecting the densities and catch rates for the different ‘years’ to Analysis of Variance (ANOVA), examination of these data demonstrated that the densities and catch rates required $\ln(x + 1)$ transformations to meet the test assumption of homogeneous dispersions among a priori groups (see Clarke and Warwick, 2001). If ANOVA detected a significant difference between the densities and/or catch rates among years ($P < 0.05$), Scheffe’s test was used to identify where the variable differed significantly between each pair of years.

3. Results

3.1. Decline in freshwater discharge and relationship with hypoxia

The annual discharge of freshwater entering the upper estuary declined markedly during the 20 years between 1992 and 2011 ($r^2 = 0.35$, $P < 0.01$). The influence of this discharge on oxygen concentrations is reflected in the close relationship between the annual values for the average extent of hypoxia and discharge ($r^2 = 0.50$, $P < 0.005$), reflecting the tight coupling between the persistence of the salt–wedge and freshwater discharge.

3.2. Body condition and growth

The three-parameter model, representing the relationship between the natural logarithms of body mass and length for females of Acanthopagrus butcheri in the Swan River Estuary in 1993–95 and 2007–11 when using linear equations with a common slope and different intercepts ($NLL = -233.2$) provided a better fit than the alternative three-parameter model, which assumed a common intercept and different slopes ($NLL = -233.0$). It also provided a significantly better fit ($P < 0.001$) than the two-parameter model that assumed a common linear relationship between body mass and length in the two periods ($NLL = -217.0$). A further increase in model complexity, by allowing both the intercepts and slopes to differ ($NLL = -233.6$), failed to produce a significant improvement in fit ($P > 0.05$). The results for males were similar to those for females, with the model assuming a common slope and different intercepts ($NLL = -229.6$) producing a slightly better fit to the data than that assuming a common intercept and different slopes ($NLL = -229.3$) and improving the fit significantly ($P < 0.001$) over that provided by the model with a common slope and common intercept ($NLL = -216.4$). Again, extension of the model to allow both the intercepts and slopes to differ ($NLL = -229.9$) failed to significantly improve the fit ($P > 0.05$). Thus, the linear relationships between the natural logarithms of body mass and total length for each sex in 1993–95 and 2007–10 were best represented by equations with different intercepts and a common slope (Table 1).

The mean values of the allometric condition factors for each sex in 1993–95 differed significantly (both $P < 0.001$) from those in 2007–11 (Table 1). The power terms of the length–weight relationships for neither sex differed significantly between 1993–95 and 2007–11, the allometric condition factors for fish from the two periods were directly comparable as a common power term could be employed to calculate their values. Thus, between 1993–95 and 2007–11 the expected values of the allometric condition factor for females and males declined by 6% and 5%, respectively.

The von Bertalanffy growth curves provided a good fit to the vast majority of the lengths at ages of both the females and males of A. butcheri.
Table 1
Estimated values of parameters of relationships (W = \(a_{\text{period}}L_{\infty,\text{period}}^{b_{\text{period}}}\)) between body mass (g), W, and total length (mm), L, for Acanthopagrus butcheri collected from the Swan River Estuary in 1993–95 and 2007–11, with estimates of expected values of the allometric condition factors for these periods, \(CF_{\text{period}}\), and with bootstrap estimates of approximate 95% confidence intervals.

<table>
<thead>
<tr>
<th>Year</th>
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<tr>
<td></td>
<td>(a_{\text{period}})</td>
<td>(b_{\text{period}})</td>
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<tr>
<td>1993–95</td>
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<td>1.152 \times 10^{-5}</td>
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<tr>
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<td>2007–11</td>
<td>3.080 \times 10^{-6}</td>
<td>3.116 \times 10^{-5}</td>
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</tbody>
</table>

Acanthopagrus butcheri in 1993–95 and 2007–11 (Table 2; Fig. 4). The curve for the females in 1993–95 lay above and differed significantly (\(P < 0.001\)) from that of this sex in 2007–11 and the same was true for those of males in these two periods (Fig. 5). Furthermore, the growth parameters \(k\) and \(L_{\infty}\) for each sex differed significantly between the two periods (all \(P < 0.001\)) and were less in 2007–11 than in 1993–95. The values for the \(t_0\) of both sexes were slightly more negative in 2007–11 than in 1993–95 (both \(P < 0.001\)). Based on the von Bertalanffy growth parameters, the TLs of female A. butcheri at ages two and six years were 142 and 248 mm, respectively, in 2007–11 and thus far less than the corresponding TLs of 203 and 366 mm in 1993–95. Likewise, the estimated TLs of males of 144 and 235 mm, respectively, at those same ages in 2007–11 were far less than the corresponding values of 199 and 354 mm in 1993–95.

Table 2
von Bertalanffy growth curve parameters and their 95% confidence intervals for females and males of Acanthopagrus butcheri caught in the upper Swan River Estuary in 1993–95, 2003–04 and 2007–11. \(L_{\infty}\), asymptotic total length (mm); \(k\), growth coefficient (years\(^{-1}\)); \(t_0\), hypothetical age (years) at which fish would have zero length; \(r^2\), coefficient of determination. \(n\) is the number of fish.

<table>
<thead>
<tr>
<th>Year</th>
<th>(L_{\infty})</th>
<th>(k)</th>
<th>(t_0)</th>
<th>(r^2)</th>
<th>(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993–95</td>
<td>Estimate</td>
<td>Lower</td>
<td>Upper</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>441</td>
<td>427</td>
<td>454</td>
<td>0.29</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>0.29</td>
<td>0.19</td>
<td>-0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>424</td>
<td>413</td>
<td>436</td>
<td>0.29</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>0.19</td>
<td>-0.13</td>
<td>-0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003–04</td>
<td>Estimate</td>
<td>Lower</td>
<td>Upper</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>322</td>
<td>284</td>
<td>371</td>
<td>0.35</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>0.35</td>
<td>-0.21</td>
<td>-0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>351</td>
<td>279</td>
<td>300</td>
<td>0.28</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>0.28</td>
<td>-0.42</td>
<td>-0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2007–11</td>
<td>Estimate</td>
<td>Lower</td>
<td>Upper</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>341</td>
<td>321</td>
<td>362</td>
<td>0.19</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>0.19</td>
<td>-0.92</td>
<td>-0.76</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>288</td>
<td>274</td>
<td>306</td>
<td>0.25</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>0.25</td>
<td>-0.85</td>
<td>-0.68</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The growth curves for the more limited samples for females and males in 2003–04 lay between and differed significantly from those for the corresponding sex in 1993–95 and 2007–11 (Fig. 5, all \(P < 0.001\)). In the case of each sex, the value for \(k\) in 2003–04 differed significantly from that in 2007–11 (both \(P < 0.001\)), and the same was true for females for 2003–04 vs 1993–95 (\(P < 0.05\)).

Fig. 4. von Bertalanffy growth curves for female and male Acanthopagrus butcheri caught in the Swan River Estuary in 1993–95, 2003–04 and 2007–11.

Fig. 5. Comparisons of von Bertalanffy growth curves for females and the males of Acanthopagrus butcheri in the Swan River Estuary during 1993–95, 2003–04 and 2007–11.


\[ L_\infty \text{ for females and males in 2003–04 each differed significantly from that of the corresponding sex in 1993–95 and 2007–11 (all } P < 0.001\text{), except with females in 2003–04 vs 2007–11 (} P > 0.05\text{). The values for } t_0 \text{ in 2003–04 were significantly different from those for females (} P < 0.001\text{) and males (} P < 0.05\text{) in 2007–11.}

3.3. Lengths and ages at maturity

The smallest TL of the mature females and males of Acanthopagrus butcheri during the spawning period were 170 and 151 mm, respectively, in 1993–94, and 144 and 143 mm, respectively, in 2007–10. As the prevalence of mature females and males increased with length, the percentage of mature individuals in each corresponding length class was less in 1993–94 than in 2007–10 (Fig. 6). The ogive describing the relationship between the proportion of mature females and total length in 1993–94 differed from that for 2007–10 (NLL = 77.4 vs 80.7 for a common curve, } P < 0.05\text{), while the corresponding ogives for males for the two periods were not significantly different (NLL = 54.8 vs 56.3, } P > 0.05\text{). Although the } L_{SO5} \text{ at maturity of neither sex differed significantly between 1993–94 and 2007–10 (both } P > 0.05\text{), the values for females and males in 1993–94, i.e. 174 and 172 mm, were substantially greater than the 156 and 155 mm for the corresponding sex in 2007–10 (Table 3, Fig. 6).

Only one fish had reached maturity by the end of its first year of life in 2007–10 (Fig. 7). However, while most females and males had become mature at the end of their second year of life in 1993–94, only 56% of females and 35% of males had attained maturity at this age in 2007–10 (Fig. 7). The ogives describing the relationships between the proportion of mature females and age in 1993–94 and 2007–10 were significantly different (NLL = 54.4 vs 84.2, } P < 0.001\text{) and the same was true for males (NLL = 91.8 vs 101.4, } P < 0.001\text{). The } A50 \text{ of 1.9 years for females at maturity in 1993–94 was significantly less than the 2.5 years for female at maturity in 2007–10 (} P < 0.001\text{) and the same significant trend (} P < 0.001\text{) was exhibited by the corresponding values of 2.0 and 2.5 years for males at maturity in those periods (Table 3, Fig. 7).

3.4. Catch rates in deeper waters and densities in shallow water

ANOVA demonstrated that the mean annual catch rates of Acanthopagrus butcheri, derived from samples obtained using gill nets at nine sites in offshore, deeper waters, differed significantly among years (} F (5, 186) = 4.4, } P < 0.01\text{). Mean catch rates ranged downwards from a maximum of 3.7 fish net\(^{-1}\) in 1993–94 to a minimum of 0.3 fish net\(^{-1}\) in 2007–08 (Fig. 8), with Scheffé’s test showing that the mean catch rates in 1993–94 and in 2007–08 were significantly different (} P < 0.01\text{). The mean densities of Acanthopagrus butcheri, derived from samples obtained using a 41.5 m seine net at six sites in nearshore waters, differed significantly among years (} F(6, 17) = 13.2, } P < 0.001\text{). The mean densities in 1993–94 and 1994–95 were <1.0 fish 100 m\(^{-2}\) and thus far less than in 2003–04 and 2007–08–2010–11, when they ranged from 4.6 to 8.4 fish 100 m\(^{-2}\) (Fig. 8). The mean density of fish in 1993–94 and 1994–95 differed significantly from those in 2003–04, 2007–08, 2009–10 and 2010–11 and that in 1994–95 was greater than those in 2003–04 and 2007–08–2010–11 (} P < 0.001–0.05\text{).

Table 3

<table>
<thead>
<tr>
<th>Period</th>
<th>Sex</th>
<th>Statistic</th>
<th>} L_\infty \text{ (mm)}</th>
<th>} L_50 \text{ (mm)}</th>
<th>} A50 \text{ (y)}</th>
<th>} A95 \text{ (y)}</th>
<th>} n_{length}</th>
<th>} n_{age}</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993–95</td>
<td>Females</td>
<td>ML estimate</td>
<td>174</td>
<td>210</td>
<td>1.9</td>
<td>2.2</td>
<td>156</td>
<td>103</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lower</td>
<td>159</td>
<td>194</td>
<td>1.6</td>
<td>2.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Upper</td>
<td>187</td>
<td>234</td>
<td>2.0</td>
<td>2.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>ML estimate</td>
<td>172</td>
<td>189</td>
<td>2.0</td>
<td>2.1</td>
<td>196</td>
<td>136</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lower</td>
<td>152</td>
<td>175</td>
<td>1.4</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Upper</td>
<td>181</td>
<td>206</td>
<td>2.0</td>
<td>2.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2007–10</td>
<td>Females</td>
<td>ML estimate</td>
<td>156</td>
<td>188</td>
<td>2.5</td>
<td>3.7</td>
<td>422</td>
<td>422</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lower</td>
<td>151</td>
<td>175</td>
<td>2.4</td>
<td>3.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Upper</td>
<td>161</td>
<td>190</td>
<td>2.7</td>
<td>3.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>ML estimate</td>
<td>155</td>
<td>182</td>
<td>2.5</td>
<td>3.5</td>
<td>329</td>
<td>329</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lower</td>
<td>150</td>
<td>171</td>
<td>2.3</td>
<td>3.0</td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Upper</td>
<td>160</td>
<td>184</td>
<td>2.7</td>
<td>3.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Please cite this article in press as: Cottingham, A., et al., Marked deleterious changes in the condition, growth and maturity schedules of Acanthopagrus butcheri (Sparidae) in an estuary reflect environmental degradation, Estuarine, Coastal and Shelf Science (2014), http://dx.doi.org/10.1016/j.ecss.2014.07.021
4. Discussion

The deleterious environmental changes that have occurred in the Swan River Estuary over the last twenty years, and in particular the increase in hypoxia, form part of a widespread trend of similar degradation (Vaquer-Sunyer and Duarte, 2008; Friedrich et al., 2014; Bruce et al., 2014). Indeed, Diaz (2002) has stated that "no other environmental variable of such ecological importance to estuarine and coastal marine ecosystems around the world has changed so drastically, in such a short period of time, as dissolved oxygen". He points out that the oxygen budgets in many coastal ecosystems have been so adversely affected through the process of eutrophication (production of excess organic material) that they could lead to the loss of fisheries and biodiversity and alteration of food webs.

As Acanthopagrus butcheri is typically confined to its natal estuary for the whole of its life cycle, the individuals of this species are potentially exposed, throughout their life, to any ongoing deleterious changes in the environmental quality within the estuary. This feature, allied with its plastic biological characteristics, makes A. butteri an ideal candidate for exploring the ways and extent to which certain key biological characteristics of a fish species respond to detrimental changes in its environment.

The present study provides the first demonstration that the condition factor, growth and maturity indices of a fish species, whose entire life cycle is confined to estuaries, have all changed in association with marked detrimental modifications to the environment. Furthermore, each change was shown to occur in the direction hypothesised from the results of other relevant studies (see below) and the model of Stearns (1992). When considering the implications of the inter-period comparisons of particularly the growth of Acanthopagrus butcheri, it is important to recognise that the growth curves for 1993–95 and for 2007–11 represent the cumulative effects of the growth of the individuals during those periods and, in the case of older fish, that which occurred prior to the commencement of those two periods. The possibility that changes in the biological characteristics of A. butcheri were induced by an increase in intensity of fishing, as described for a number of other species (e.g. Sharpe and Hendry, 2009; Devine et al., 2012; Diaz and Heino, 2014), can be rejected for the following reasons. The small seasonal commercial fishery for A. butcheri in the Swan River Estuary has been negligible since 2007, due to a government buy-back of commercial fishing licences (Smith et al., 2013), and the recreational catch per unit effort data indicate that the abundance of A. butteri has remained relatively stable since the early 1990s (Smith, 2006; Smith et al., 2013).
4.1. Condition and growth

As condition is a reliable indicator of the health of a fish (Peig and Green, 2009), it is highly relevant that the allometric condition factor for female and male Acanthopagrus butcheri in the upper Swan River Estuary declined significantly between 1993–95 and 2007–11. Furthermore, this decline in condition was accompanied by a marked reduction in the growth of both sexes, with the growth curve for the intervening 2003–04 period occupying an approximately intermediate position between the earlier and later periods. Indeed, on the basis of von Bertalanffy growth parameters, the predicted lengths at two and six years in age declined between 1993–95 and 2007–11 by as much as 32 and 34%, respectively, with females, and by 67 and 73%, respectively, with males.

The significant decline in the condition factor and growth of Acanthopagrus butcheri in the Swan River Estuary between 1993–95 and 2007–11 parallels the observation by Eby et al. (2005) that the condition and growth of the Atlantic croaker Micropogonias undulatus in the Neuse River Estuary was least in years when the extent of hypoxia was greatest. The results of controlled laboratory experiments, in which M. undulatus was exposed to four and ten weeks of hypoxia subsequently supported the conclusion that the density-dependent effects for this species can be visibly affected by reduced oxygen concentrations (Mohan et al., 2014). A number of laboratory studies on other fish species have produced similar results, particularly with growth (e.g. Kramer, 1987; Pichavant et al., 2001; Roberts et al., 2011). Declines in the condition and growth of fishes exposed to hypoxia have been attributed, inter alia, to a reduction in metabolism and changes in the quantity and quality of potential food (Pichavant et al., 2001; Wu, 2002; Eby et al., 2005; Powers et al., 2005). In the context of food, the volumetric contributions made to the diets of A. butcheri in the Swan River Estuary by low-calorie food, such as algae, macrophytes and detritus, increased from 15 to 30% between 1993–95 and 2007–11, whereas high-calorie prey, such as bivalve molluscs, declined from 64 to 19% (cf Sarre et al., 2000; Linke, 2011). These trends parallel those recorded during studies of M. undulatus in the Neuse River Estuary, which showed that, following exposure to hypoxia, the density of food and particularly of bivalves (Macoma spp.) declined and was thus considered to be one of the factors that led to reductions in the growth (Eby et al., 2005). Unfortunately, there are no quantitative data to facilitate comparisons between the quantity and quality of the benthic macroinvertebrates and macroalgae of A. butcheri in offshore and nearshore waters in the two periods and which are known to constitute the diet of this species (Sarre et al., 2000; Chuwen et al., 2007).

In the context of factors that could also have attributed to the decline in the condition and growth of Acanthopagrus butcheri between 1993–95 and 2007–11, it is pertinent that data, derived from gill and seine net catches, provided strong circumstantial evidence that the abundance of A. butcheri in offshore, deeper waters has declined, whereas that in nearshore, shallow waters has increased markedly. This therefore constitutes habitat compression of the type induced by hypoxia among demersal fish in the Neuse River Estuary on the east coast of North America (Eby et al., 2005), pelagic fish in tropical waters in the eastern Pacific (Prince and Goodyear, 2006) and certain species in other environments (e.g. Pihl et al., 1991; Tyler and Targett, 2007; Craig, 2012). A tendency, during the past 10–20 years, for A. butcheri to have moved from deeper to shallower waters, and the demonstration that its density in the latter waters has become far greater, raises the strong possibility that this density-dependent factor has also played an important role in leading to a decline in the growth of this species over time. It is thus noteworthy that density dependent factors were also considered responsible for the decline in growth of Micropogonias undulatus in the Neuse River Estuary (Eby et al., 2005). In addition, the use of fishery-independent data demonstrated that the growth of the 0+ and 1+ age classes of the red drum Sciaenops ocellatus were negatively related to the density of their own age classes (Bacheler et al., 2012). Furthermore, analysis of long-term records of size at age and biomass data for 16 fish populations revealed that the growth of individuals in nine of those populations was inversely related to density (Lorenzen and Enberg, 2002).

4.2. Length and age at maturity

As the ogives relating maturity to length in females and to age in both sexes of Acanthopagrus butcheri differed significantly between 1993–94 and 2007–10, the maturity characteristics of this species have typically changed between the two periods. It was particularly striking that, between 1993–94 and 2007–10, the L50 of females and males at maturity declined by 11 and 12%, respectively, whereas, in contrast, the A50 of females and males at maturity increased by the equivalent of 32 and 25%, respectively. The direction of the changes between the two periods is consistent with the model of Stearns (1992), which predicted that reductions in growth will lead to maturity occurring at a smaller size and older age (see also Chen and Mello, 1999; Morgan and Colbourne, 1999). This finding is also consistent with the results of a three year tag-recapture study, which demonstrated that the slower-growing residents of the white spotted char Salvelinus leucomaenis reached maturity at a smaller size but older age than faster-growing individuals, a feature considered to reflect adaptive phenotypic plasticity (Morita and Morita, 2002). For A. butcheri, the changes in both the length and age at maturity were pronounced and developed within a relatively short period, highlighting the plasticity of the biological characteristics of this species and thus its ability to respond to the effects of environmental change. This ability helps account for A. butcheri remaining abundant in the upper Swan River Estuary, even though conditions there have deteriorated over the past 20 years.

In summary, the results of this study demonstrate that the deleterious changes that have occurred in the environmental conditions of the permanently-open microtidal Swan River Estuary since the 1990s have been accompanied by significant changes in the biological characteristics of Acanthopagrus butcheri. The marked decline in the condition and growth of A. butcheri is consistent with the known effects of hypoxia, which result in inter alia reductions in metabolism and changes in the quantity or quality of food. The declines in condition and growth between the two periods are, however, also considered to reflect density-dependent effects as fish have increasingly tended to aggregate inshore. The reduction in growth would also account for A. butcheri attaining maturity at a smaller size and older age. The results of this study thus contribute to our understanding of how, and the extent to which environmental degradation can influence the biological characteristics of a demersal fish species and will thus be of value to fisheries and environmental managers when considering the changes that could occur with other species exposed to the impacts of a decline in water quality.

Acknowledgements

Gratitude is expressed to Gavin Sarre and Steeg Hoeksema for data for A. butcheri in earlier periods and to many colleagues and friends who helped with sampling and, in particular, Amanda Buckley and Chris Hallett. Our gratitude is also expressed to Drs K. Smith and B. Wise and two anonymous referees for their constructive comments and criticisms which resulted in a substantially improved paper. Financial and other support was

<table>
<thead>
<tr>
<th>Sampling season</th>
<th>Period</th>
<th>Net type</th>
<th>Number of sites</th>
</tr>
</thead>
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<td>1993–95</td>
<td>41.5 m seine 6</td>
<td>6 (lower sites)</td>
</tr>
<tr>
<td>Spring 1993–Summer 1997</td>
<td>1993–97</td>
<td>41.5 m seine 6</td>
<td>6 (lower sites)</td>
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<tr>
<td>Summer 2000–Spring 2000</td>
<td>2000</td>
<td>Gill (catch rate)</td>
<td>9</td>
</tr>
<tr>
<td>Spring 2003–Winter 2004</td>
<td>2003–04</td>
<td>41.5 m seine 6</td>
<td>6 (lower sites)</td>
</tr>
<tr>
<td>Winter 2007–2009</td>
<td>2007–11</td>
<td>41.5 m seine 6</td>
<td>6 (lower sites)</td>
</tr>
<tr>
<td>Winter 2009–2011</td>
<td>2009–11</td>
<td>41.5 m seine 6</td>
<td>6 (lower sites)</td>
</tr>
</tbody>
</table>


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