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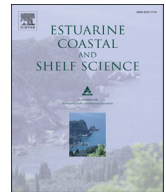
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Marked deleterious changes in the condition, growth and maturity schedules of *Acanthopagrus butcheri* (Sparidae) in an estuary reflect environmental degradation

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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_{∞} in the von Bertalanffy growth curves of both sexes underwent marked reductions. The predicted lengths of females and males at all ages ≥ 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_{50} 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

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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; Breitbart 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 to 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; Hallegraeff 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 (Twomey and John, 2001), some of which are toxic (Orr et al., 2004; Mooney et al. 2009) and have resulted in an increased prevalence of 'kills' of 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 (Sarre 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; Burrige and Versace, 2006). The 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 Hyndes, 1999; Sarre 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 (Burrige and Versace, 2006).

As with other sparids, the biological characteristics of *Acanthopagrus butcheri* are plastic, varying markedly among estuaries with different environmental characteristics. Thus, for example, among four south-western Australian estuaries, the total lengths reached after three years ranged widely from 146 to 266 mm (Sarre and Potter, 2000) and the L_{50} s and A_{50} s 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 (Sarre 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 (Sarre 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

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 above 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 monthly 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, $W = a_{\text{period}} L^{b_{\text{period}}}$, were estimated by fitting linear equations of the form: $\ln(W_j) = \ln(a_{\text{period}}) + b_{\text{period}} \ln(L_j) + \varepsilon_{\text{period},j}$, to the masses (g) and

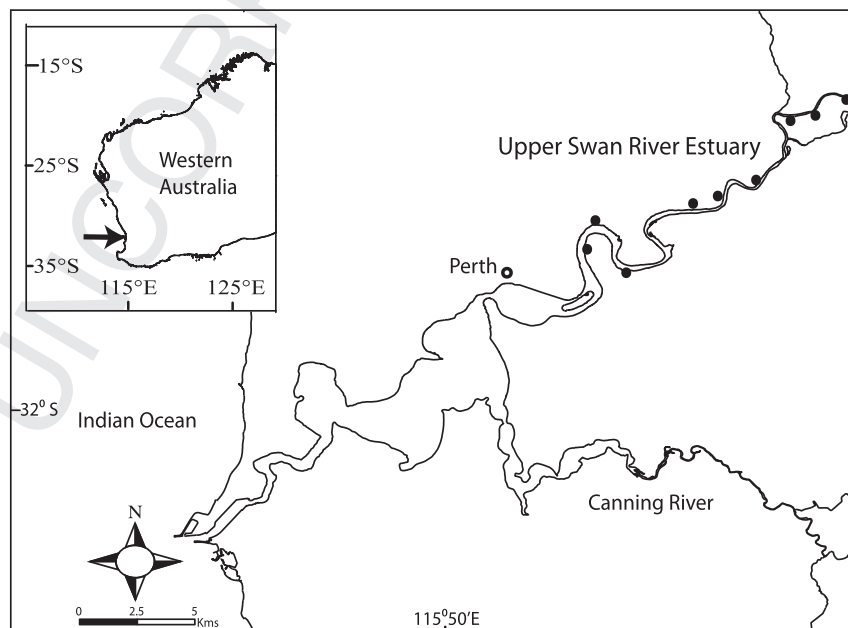


Fig. 1. Map showing sites (closed circles) at which *Acanthopagrus butcheri* was sampled by seine and gill nets in the upper Swan River Estuary. Arrow in insert map shows the location of the Swan River Estuary in Western Australia.

total lengths (mm) for the 90 females and 90 males in the 2007–11 and 1993–95 periods. In this latter equation, \ln refers to the natural logarithm, W_j and L_j are the observed mass and length, respectively, of the j 'th fish, and the deviations of the logarithms of the observed masses from the values predicted by the regression equations were assumed to be normally distributed with means of zero and variances that differed between the two periods, i.e. $\varepsilon_{\text{period},j} \sim N(0, \sigma_{\text{period}}^2)$. In the case of both sexes, the linear equations were fitted simultaneously to the data for the two periods using R (R Core Team, 2013). Likelihood-ratio tests were employed to compare, for each sex, the model that assumed a common length–weight relationship for the two periods against the best fitting (i.e. smaller negative log-likelihood, NLL) of the two three-parameter models, which assumed that either the slope or the intercept (but not both) remained constant, and that latter model against the model that assumed that both the intercept and slope of the regression equation differed between the two periods. Approximate 95% confidence intervals for a_{period} and b_{period} were estimated as the 2.5 and 97.5 percentiles of the distributions of 1000 parameter estimates obtained by drawing (with replacement) a sample from the data for each sex and period (with the same sample size as the original sample) and refitting the linear regression equation to that sample. When calculating the expected masses of fish from their total lengths, the correction factor $\exp(\hat{\sigma}_{\text{period}}^2/2)$ was employed (Beauchamp and Olson, 1973) to account for the bias associated with back-transformation of the predicted values from the values of their natural logarithms. Thus, for each period and sex, the back-transformed allometric equation became $W = [a_{\text{period}} \exp(\hat{\sigma}_{\text{period}}^2/2)] L^{b_{\text{period}}}$, where $\hat{\sigma}_{\text{period}}^2$ is the estimated variance of the residuals from the fitted linear equation.

The allometric condition factor, CF_j , for fish j of mass W_j and total length L_j for each period and sex was calculated as $CF_j = W_j/L_j^{b_{\text{period}}}$ using the value of b_{period} that was estimated for the length–weight relationship for that period (Tesch, 1968). A t -test was used to compare, for each sex, the mean value of the resulting estimates of CF for 2007–11 with that for 1993–95. As $W_j = a_{\text{period}} L_j^{b_{\text{period}}} \exp(\varepsilon_j)$, where $\varepsilon_j \sim N(0, \sigma_{\text{period}}^2)$, the expected value of CF_j for the period and sex was calculated as $\overline{CF}_{\text{period}} = a_{\text{period}} \exp(\sigma_{\text{period}}^2/2)$. Approximate 95% confidence intervals for $\overline{CF}_{\text{period}}$ were calculated for each period and sex from the 1000 bootstrapped samples that were drawn to estimate the confidence intervals for the parameters a_{period} and b_{period} of the weight–length relationships.

2.3. Growth

The otoliths of all *Acanthopagrus butcheri* were initially examined whole using a dissecting microscope under reflected light. The number of opaque zones on otoliths containing ≤ 6 such zones were counted on whole otoliths. N. B. Sarre and Potter (2000) had demonstrated that the counts of opaque zones on whole otoliths with ≤ 6 zones were the same as those obtained using sectioned otoliths, but that this was occasionally not the case when otoliths contained > 6 zones. All otoliths with > 6 opaque zones were thus sectioned prior to counting their opaque zones (see Sarre and 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. N.B. marginal increment analyses by Sarre and 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 the otoliths of that fish, the date

of capture of the fish 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 has typically become delineated from the periphery of the otolith by the beginning of November.

The number of opaque zones in each of 200 randomly-selected otoliths of *Acanthopagrus butcheri*, which covered a wide size range, was counted independently by A. Cottingham and A. Hesp and the counts compared using the coefficient of variation (CV) (see Chang, 1982; Campana, 2001). The resultant CV of 2.0% is well below the cut-off point of 5% considered acceptable for replicate ageing of medium to long-lived species (Campana, 2001), demonstrating a high level of consistency between the counts of the two readers.

Using non-linear regression, the von Bertalanffy growth model (VBGM) 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 $\hat{L}_t = L_{\infty} [1 - \exp(-k(t - t_0))]$, where \hat{L}_t is the expected total length at age t (years), L_{∞} 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/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 $P = 1/[1 + \exp\{-\ln(19)(L - L_{50})/(L_{95} - L_{50})\}]$, where L is the total length of the fish in mm and L_{50} and L_{95} are the lengths at which 50 and 95% of fish attain maturity, respectively. The values of L_{50} and L_{95} were estimated by minimising the negative log-likelihood (NLL) using R (R Core Team, 2013). Likelihood-ratio tests were used to determine whether, for each sex, the ogives relating maturity to length in 1993–94 and 2007–10 were different and, if so, whether this could be attributed to a difference in the values of L_{50} . The analysis was repeated using OpenBUGS (Surhone et al., 2010), a successor to WinBUGS (Lunn et al., 2000), with two chains, 1,004,000 iterations, a burn-in of 1000 and a thinning interval of 20, to obtain estimates of the approximate 95% credible intervals for L_{50} and L_{95} and the expected proportion of mature fish at each of a range of total

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_{50} . 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 season 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 ($P < 0.05$), Scheffé'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 (Fig. 2, $r^2 = 0.35$, $P < 0.01$). 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 (Fig. 3, $r^2 = 0.50$, $P < 0.005$), 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

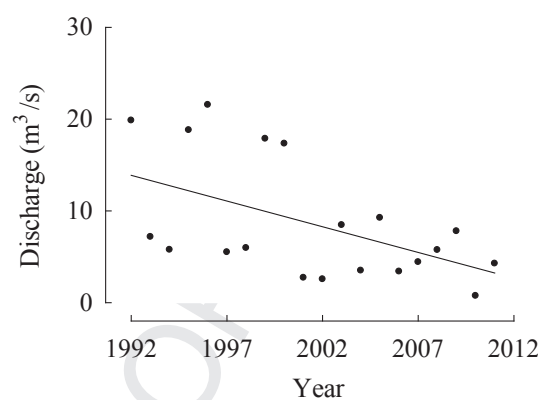


Fig. 2. Freshwater discharge into the Swan River Estuary in the 20 years between 1992 and 2011. Data provided by the Western Australian Department of Water.

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). As 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

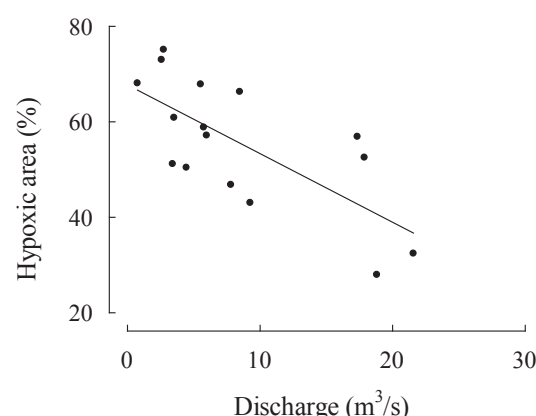


Fig. 3. Relationship between the annual average extent of hypoxia (%) in the upper Swan Estuary and freshwater discharge between 1995 and 2010. The extent of hypoxia in each year was estimated by interpolating available oxygen profile data for each sampling cruise within the study domain for each weekly profile and then averaging the values for each year.

Table 1

Estimated values of parameters of relationships ($W = a_{\text{period}} L^{b_{\text{period}}}$ QUOTE) 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, QUOTE $\overline{CF}_{\text{period}}$, and with bootstrap estimates of approximate 95% confidence intervals.

		Females		Males	
		1993–95	2007–11	1993–95	2007–11
a_{period}	Estimate	9.370×10^{-6}	8.833×10^{-6}	1.147×10^{-5}	1.086×10^{-5}
	Lower	7.603×10^{-6}	7.153×10^{-6}	9.389×10^{-6}	8.921×10^{-6}
	Upper	1.152×10^{-5}	1.091×10^{-5}	1.423×10^{-5}	1.350×10^{-5}
b_{period}	Estimate	3.116	3.116	3.080	3.080
	Lower	3.076	3.076	3.040	3.040
	Upper	3.155	3.155	3.116	3.116
$\overline{CF}_{\text{period}}$	Estimate	9.391×10^{-6}	8.851×10^{-6}	1.149×10^{-5}	1.089×10^{-5}
	Lower	7.622×10^{-6}	7.170×10^{-6}	9.408×10^{-6}	8.942×10^{-6}
	Upper	1.155×10^{-5}	1.093×10^{-5}	1.426×10^{-5}	1.353×10^{-5}

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_{∞} 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_{∞} , 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.

Year	L_{∞}	k	t_0	r^2	n
1993–95					
Females					
Estimate	441	0.29	-0.12	0.94	680
Lower	427	0.27	-0.19		
Upper	454	0.31	-0.06		
Males					
Estimate	424	0.29	-0.19	0.99	754
Lower	413	0.27	-0.26		
Upper	436	0.31	-0.13		
2003–04					
Females					
Estimate	322	0.35	-0.13	0.96	111
Lower	284	0.26	-0.21		
Upper	371	0.44	-0.06		
Males					
Estimate	351	0.28	-0.28	0.99	88
Lower	279	0.19	-0.42		
Upper	300	0.42	-0.13		
2007–11					
Females					
Estimate	341	0.19	-0.84	0.89	3438
Lower	321	0.17	-0.92		
Upper	362	0.22	-0.76		
Males					
Estimate	288	0.25	-0.76	0.90	3248
Lower	274	0.22	-0.85		
Upper	306	0.28	-0.68		

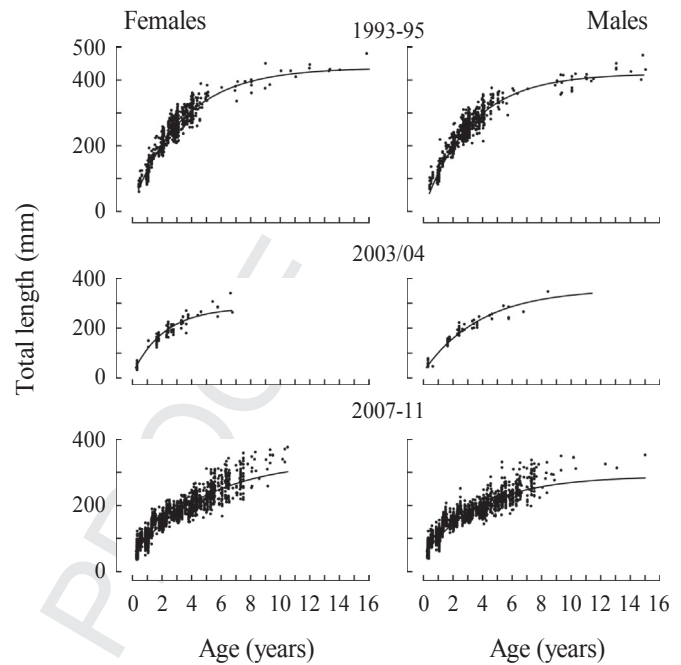


Fig. 4. von Bertalanffy growth curves for female and male *Acanthopagrus butcheri* caught in the Swan River Estuary in 1993–95, 2003–04 and 2007–11.

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 ($P < 0.05$). The

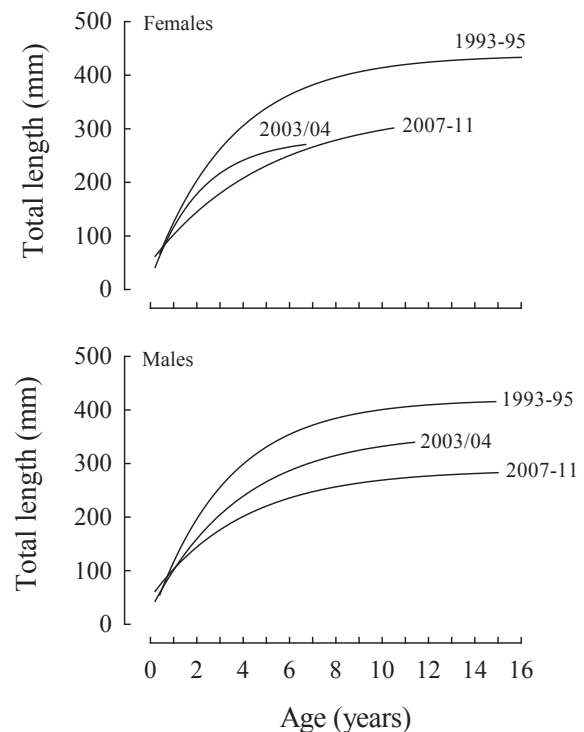


Fig. 5. Comparisons of von Bertalanffy growth curves for females and the males of *Acanthopagrus butcheri* in the Swan River Estuary during 1993–95, 2003–04 and 2007–11.

L_{∞} for females and males in 2003–04 each differed significantly from that of the corresponding sex in 1993–95 and 2007–11 (all $P < 0.001$), except with females in 2003–04 vs 2007–11 ($P > 0.05$). The values for t_0 in 2003–04 were significantly different from those for females ($P < 0.001$) and males ($P < 0.05$) 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, $P < 0.05$), while the corresponding ogives for males for the two periods were not significantly different (NLL = 54.8 vs 56.3, $P > 0.05$). Although the L_{50} s at maturity of neither sex differed significantly between 1993–94 and 2007–10 (both $P > 0.05$), 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, $P < 0.001$) and the same was true for males (NLL = 91.8 vs 101.4, $P < 0.001$). The A_{50} 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 ($P < 0.001$) and the same significant trend ($P < 0.001$) 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 ($F(5, 186) = 4.4$, $P < 0.01$). 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 ($P < 0.01$).

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 ($F(6, 17) = 13.2$, $P < 0.001$). 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).

Table 3

Estimates of the total lengths (mm) and ages (years), and associated 95% credible intervals, at which 50% (L_{50} and A_{50}) and 95% (L_{95} and A_{95}) of female and male *Acanthopagrus butcheri* were mature in the Swan River Estuary in 1993–95 and in 2007–10. ML = Maximum likelihood. Lower and upper credible limits were determined using OpenBUGS. n is the number of fish.

Period	Sex	Statistic	L_{50} (mm)	L_{95} (mm)	A_{50} (y)	A_{95} (y)	n_{length}	n_{age}
1993–95	Females	ML estimate	174	210	1.9	2.2	156	103
		Lower	159	194	1.6	2.0		
		Upper	187	234	2.0	2.6		
	Males	ML estimate	172	189	2.0	2.1	196	136
		Lower	152	175	1.4	1.8		
		Upper	181	206	2.0	2.2		
2007–10	Females	ML estimate	156	188	2.5	3.7	422	422
		Lower	151	175	2.4	3.2		
		Upper	161	190	2.7	3.8		
	Males	ML estimate	155	182	2.5	3.5	329	329
		Lower	150	171	2.3	3.0		
		Upper	160	184	2.7	3.6		

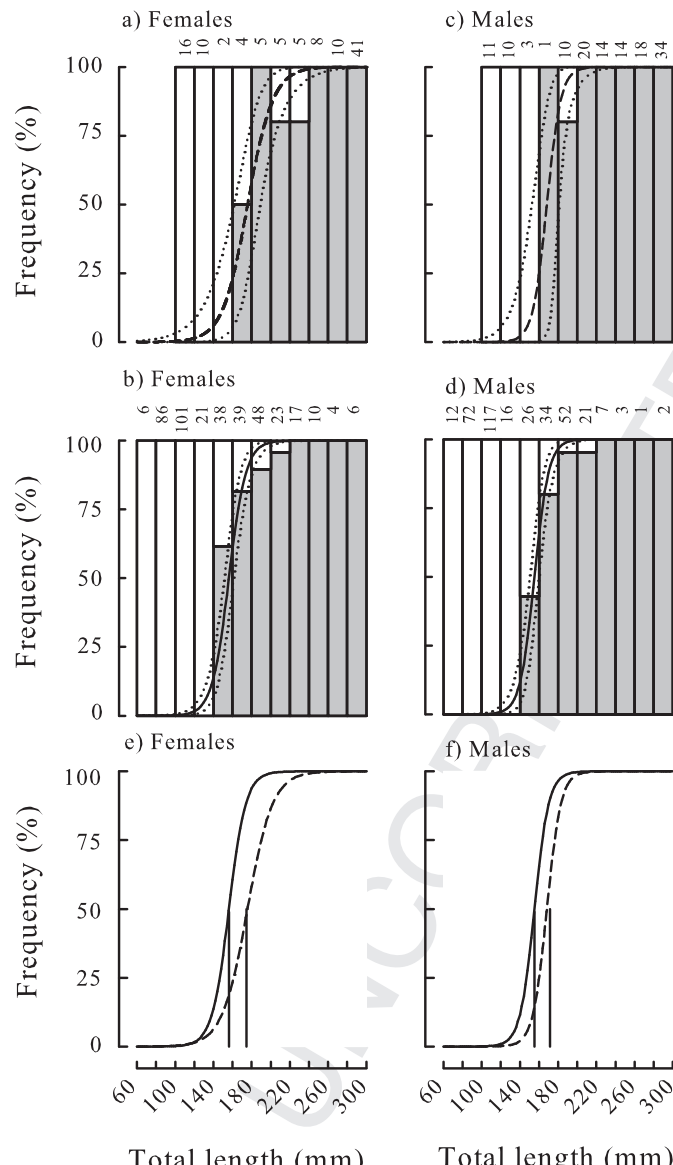


Fig. 6. Percentage frequency of occurrence of *Acanthopagrus butcheri* with immature (white bars) and mature gonads (grey bars) in sequential 20 mm total length classes during the spawning seasons of this species in the Swan River Estuary in different years. Females in (a) 1993 and 1994 collectively and (b) 2007–10 and males in (c) 1993 and 1994 collectively and (d) 2007–10. Logistic curves (solid lines) and their 95% confidence intervals (dotted lines) were derived from the probability that a fish at a given length is mature. Sample size for each length class is shown. Comparisons of the logistic curves and lengths at which 50% (vertical line) of (e) females and (f) males attained maturity in 1993–94 and in 2007–10.

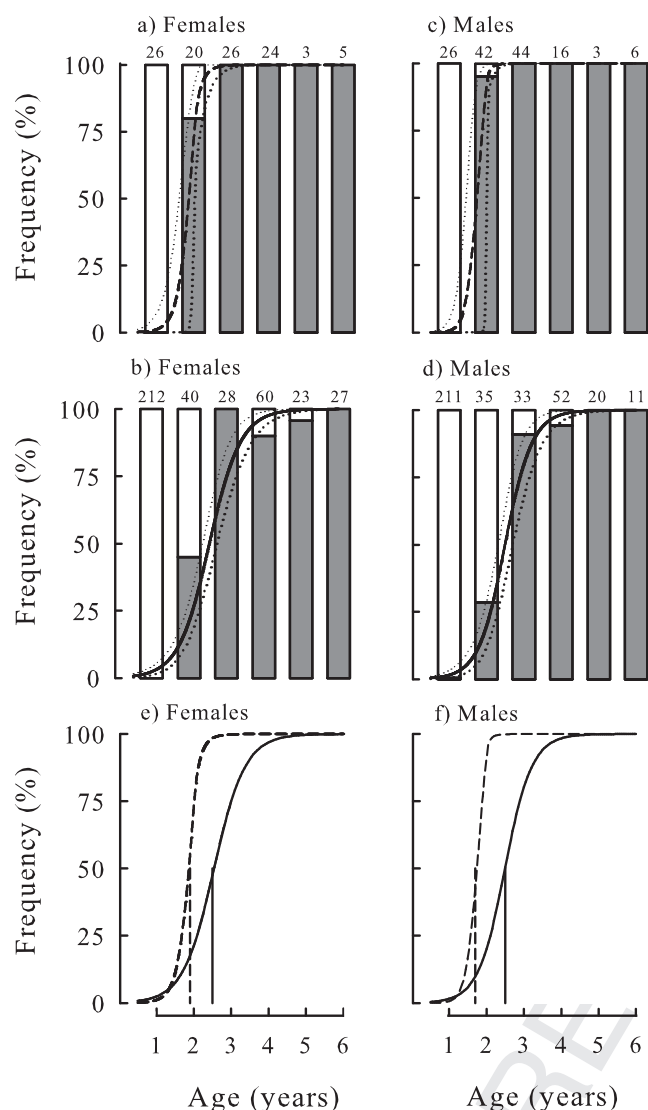


Fig. 7. Percentage frequency of occurrence of *Acanthopagrus butcheri* with immature (white bars) and mature gonads (grey bars) in sequential ages during the spawning seasons of this species in the Swan River Estuary in different years. Females in (a) 1993 and 1994 collectively and (b) 2007–10 and males in (c) 1993 and 1994 collectively and (d) 2007–10. Logistic curves (solid lines) and their 95% confidence intervals (dotted lines) were derived from the probability that a fish at a given age is mature. Sample size for each age class is shown. Comparisons of the logistic curves and ages at which 50% (vertical line) of e) females and f) males attained maturity in 1993–94 and in 2007–10.

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 worldwide 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.

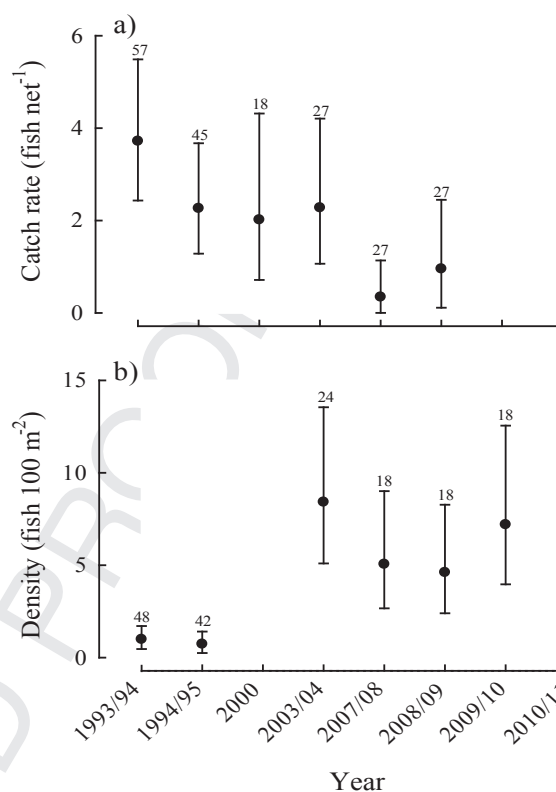


Fig. 8. Mean and associated 95% confidence intervals for a) catch rates derived from gill net samples in offshore, deeper waters and b) densities derived from seine net samples in nearshore, shallow waters of *Acanthopagrus butcheri* in the Swan River Estuary in the various years of sampling. Number of samples for each year is shown.

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. butcheri* 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. butcheri* 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 condition and growth of this species can be adversely 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 shallow waters, and the demonstration that its density in the latter waters has become far greater, raises the strong possibility that density-dependent effects may also have 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 L_{50} of females and males at maturity declined by 11 and 12%, respectively, whereas, in contrast, the A_{50} 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 charr *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.

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Appendix

Regime for sampling *Acanthopagrus butcheri* in the Swan River Estuary using seine and gill nets between 1993 and 2011.

Sampling seasons	Period	Net type	Number of sites
Spring 1993–Autumn 1995	1993–95	41.5 m seine	6 (lower sites)
Spring 1993–Summer 1995		Gill	9
Summer 2000–Spring 2000	2000	Gill (catch rate only)	9
Spring 2003–Winter 2004	2003–04	21.5 m seine	6 (lower sites)
		41.5 m seine	6 (lower sites)
		Gill	9
Winter 2007–Autumn 2009	2007–11	21.5 m seine	9
		41.5 m seine	9
		Gill	9
Winter 2009–Autumn 2011	2007–11	21.5 m seine	9
		41.5 m seine	9

References

Able, K.W., Fahay, M.P., 2010. Ecology of Estuarine Fishes: Temperate Waters of the Western North Atlantic. Johns Hopkins University Press, Baltimore, Maryland, p. 566.

Australian Bureau of Meteorology, 2014. Climate Data Online. Location: Perth Airport (accessed 25.02.14.). <http://www.bom.gov.au/climate/data/?ref=fr>.

Bacheler, N.M., Buckel, J.A., Paramore, L.M., 2012. Density-dependent habitat use and growth of an estuarine fish. *Can. J. Fish. Aquat. Sci.* 69, 1734–1747.

Beauchamp, J.J., Olson, J.S., 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology* 54, 1403–1407.

Blaber, S.J.M., Blaber, T.G., 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *J. Fish. Biol.* 17, 143–162.

Breitburg, D.L., Hondorp, D.W., Davias, L.A., Diaz, R.J., 2009. Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. *Annu. Rev. Mar. Sci.* 1, 329–349.

Bruce, L.C., Cook, P.L.M., Teakle, I., Hipsey, M.R., 2014. Hydrodynamic controls on oxygen dynamics in a riverine salt-wedge estuary, the Yarra River Estuary, Australia. *Hydrol. Earth Syst. Sci.* 18, 1–14.

Burrige, C.P., Versace, V.L., 2006. Population genetic structuring in *Acanthopagrus butcheri* (Pisces: Sparidae): does low gene flow among estuaries apply to both sexes? *Mar. Biotechnol.* 9, 33–43.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish. Biol.* 59, 197–242.

Campbell, L.A., Rice, R.A., 2014. Effects of hypoxia-induced habitat compression on growth of juvenile fish in the Neuse River Estuary, North Carolina, USA. *Mar. Ecol. Prog. Ser.* 497, 199–213.

Cerrato, R.M., 1990. Interpretable statistical test for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47, 1416–1426.

Chang, W.Y.B., 1982. A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.* 39, 1208–1210.

Chaplin, J.A., Baudains, G.A., Gill, H.S., McCulloch, R., Potter, I.C., 1998. Are assemblages of black bream (*Acanthopagrus butcheri*) in different estuaries genetically distinct? *Int. J. Salt Lake Res.* 6, 303–321.

Chen, Y., Mello, L.G.S., 1999. Growth and maturation of cod (*Gadus morhua*) of different year classes in the Northwest Atlantic, NAFO subdivision 3Ps. *Fish. Res.* 42, 87–101.

Chuwen, B.M., Platell, M.E., Potter, I.C., 2007. Dietary compositions of the sparid *Acanthopagrus butcheri* in three normally closed and variably hypersaline estuaries differ markedly. *Environ. Biol. Fish.* 80, 363–376.

Chuwen, B.M., Potter, I.C., Hall, N.G., Hoeksema, S.D., Laurensen, L.J.B., 2011. Changes in catch rates and length and age at maturity, but not growth, of an estuarine plotosid (*Cnidogobius macrocephalus*) after heavy fishing. *Fish. Bull.* 109, 247–260.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. PRIMER-E, Plymouth, U.K, p. 38.

Cloern, J.E., Foster, S.Q., Kleckner, A.E., 2013. Review: phytoplankton primary production in the world's estuarine-coastal ecosystems. *Biogeosciences Discuss.* 10, 17725–17783.

Craig, J.K., 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 445, 75–95.

Craig, J.K., Crowder, L.B., Gray, C.D., McDaniel, C.J., Henwood, T.A., Hanifen, J.G., 2001. Ecological effects of hypoxia on fish, sea turtles, and marine mammals in the northwestern Gulf of Mexico. In: Rabalais, N.N., Turner, R.E. (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. American Geophysical Union, Washington, DC, pp. 269–291.

Devine, J.A., Wright, P.J., Pardoe, H.E., Heino, M., 2012. Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. *Can. J. Fish. Aquat. Sci.* 69, 1105–1120.

Diaz, R.J., 2000. Overview of hypoxia around the world. *J. Environ. Qual.* 30, 275–281.

Diaz, R.J., 2002. Hypoxia and anoxia as global phenomena. In: Thurston, R.V. (Ed.), *Fish Physiology, Toxicology, and Water Quality, Proceedings of the Sixth International Symposium*. Ecosystems Research Division, Athens, Georgia, pp. 183–202.

Diaz, P.B., Heino, M., 2014. What can selection experiments teach us about fisheries-induced evolution? *Biol. J. Linn. Soc.* 111, 485–503.

Eby, L.A., Crowder, L.B., 2002. Hypoxia-based habitat compression in the Neuse River Estuary: context-dependent shifts in behavioral avoidance thresholds. *Can. J. Fish. Aquat. Sci.* 59, 952–965.

Eby, L.A., Crowder, L.B., McClellan, C.B., Powers, M.J., Peterson, C.H., 2005. Habitat degradation from intermittent hypoxia: impacts on juvenile fishes. *Mar. Ecol. Prog. Ser.* 291, 249–262.

Elliott, M., Whitfield, A.K., 2011. Challenging paradigms in estuarine ecology and management. *Estuar. Coast. Shelf Sci.* 94, 306–314.

Friedrich, J., Janssen, F., Aleynik, D., Bange, H.W., Boltacheva, N., Çagatay, M.N., Dale, A.W., Etiope, G., Erdem, Z., Geraga, M., Gilli, A., Gomoiu, M.T., Hall, P.O.J., Hansson, D., He, Y., Holtappels, M., Kirf, M.K., Kononets, M., Konovalov, S., Lichtschlag, A., Livingstone, D.M., Marinaro, G., Mazlumyan, S., Naeher, S., North, R.P., Papatheodorou, G., Pfannkuche, O., Prien, R., Rehder, G., Schubert, C.J., Soltwedel, T., Sommer, S., Stahl, H., Stanev, E.V., Teaca, A., Tengberg, A., Waldmann, C., Wehrli, B., Wenzhöfer, F., 2014. Investigating hypoxia in aquatic environments: diverse approaches to addressing a complex phenomenon. *Biogeosciences* 11, 1125–1259.

Froese, R., 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J. Appl. Ichthyol.* 22, 241–253.

Gomon, M., Bray, D., Kuitert, R., 2008. Fishes of Australia's Southern Coast. Reed New Holland, Sydney, p. 928.

Grover, M.C., 2005. Changes in size and age at maturity in a population of kokanee *Oncorhynchus nerka* during a period of declining growth conditions. *J. Fish. Biol.* 66, 122–134.

Hallegraef, G., Mooney, B., Evans, K., 2010. What Triggers Fish-killing *Karlodinium veneficum* Dinoflagellate Blooms in the Swan Canning River System. Swan Canning Research and Innovation Program Final Report Swan River Trust, Perth, Western Australia, p. 31.

Hamilton, D.P., Turner, J.V., 2001. Integrating research and management for an urban estuarine system: the Swan-Canning Estuary, Western Australia. *Hydrol. Process.* 15, 2383–2385.

Hassell, K.L., Coutin, P.C., Nugegoda, D., 2008a. Hypoxia, low salinity and lowered temperature reduce embryo survival and hatch rates in black bream *Acanthopagrus butcheri* (Munro, 1949). *J. Fish. Biol.* 72, 1623–1636.

Hassell, K.L., Coutin, P.C., Nugegoda, D., 2008b. Hypoxia impairs embryo development and survival in black bream (*Acanthopagrus butcheri*). *Mar. Pollut. Bull.* 57, 302–306.

Helle, J.H., Hoffman, M.S., 1998. Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean. *North Pac. Anadromous Fish. Comm. Bull.* 1, 81–89.

Hindell, J.S., Jenkins, G.P., Womersley, B., 2008. Habitat utilisation and movement of black bream *Acanthopagrus butcheri* (Sparidae) in an Australian estuary. *Mar. Ecol. Prog. Ser.* 366, 219–229.

Howell, P., Simpson, D., 1994. Abundance of marine resources in relation to dissolved oxygen in Long Island Sound. *Estuaries* 17, 394–402.

Hutchings, B., Thompson, M., 2001. The Marine and Estuarine Fishes of South-western Australia. A Field Guide for Anglers and Divers. Western Australia Museum, Perth, Western Australia, p. 103.

Jackson, R.B., Carpenter, S.R., Dahm, C.N., McKnight, D.M., Naiman, R.J., Postel, S.L., Running, S.W., 2001. Water in a changing world. *Ecol. Appl.* 11, 1027–1045.

Kennish, M.J., Townsend, A.R., 2007. Nutrient enrichment and estuarine eutrophication. *Ecol. Appl.* 17 (Suppl.), S1–S2.

Kramer, D.L., 1987. Dissolved oxygen and fish behavior. *Environ. Biol. Fish.* 18, 81–92.

Kristiana, R., Antenucci, J.P., Imberger, J., 2012. Using a multi-component indicator toward reducing phytoplankton bloom occurrences in the Swan River Estuary. *Environ. Manag.* 50, 237–256.

Lenanton, R.C.J., Ayvazian, S.G., Dibden, C.J., Jenkins, G., Sarre, G., 1999. The use of stock enhancement to improve the catch rates of black bream, *Acanthopagrus butcheri* (Munro) for Western Australian recreational fishers. In: Howell, B.R., Moksness, E., Svåsand, T. (Eds.), *Stock Enhancement and Sea Ranching*. Fishing News Books, Oxford, UK, pp. 219–230.

Linke, T.E., 2011. Trophic Interactions Among Abundant Members of the Fish Fauna in a Permanently-open and Seasonally-open Estuary in South-western Australia. Ph.D. thesis. Murdoch University, Perth, Australia. <http://researchrepository.murdoch.edu.au-12662/>.

- Lorenzen, K., Enberg, K., 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. B Biol. Sci.* 269, 49–54.
- Lunn, D.J., Thomas, A., Best, N., Spiegelhalter, D., 2000. WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* 10, 325–337.
- McLusky, D.S., Elliott, M., 2004. *The Estuarine Ecosystem: Ecology, Threats and Management*. Oxford University Press, Oxford, p. 214.
- Mohan, J., Rahman, Md. S., Thomas, P., Walther, B., 2014. Influence of constant and periodic experimental hypoxic stress on Atlantic croaker otolith chemistry. *Aquat. Biol.* 20, 1–11.
- Mooney, B.D., De Salas, M., Hallegraeff, G.M., Place, A.R., 2009. Survey for karlotoxin production in 15 species of gymnodinioid dinoflagellates (Kareniaceae, Dinophyta). *J. Phycol.* 45, 164–175.
- Morgan, M.J., Colbourne, E.B., 1999. Variation in maturity-at-age and size in three populations of American plaice. *ICES J. Mar. Sci.* 56, 673–688.
- Morita, K., Fukuwaka, M., 2007. Why age and size at maturity have changed in Pacific salmon. *Mar. Ecol. Prog. Ser.* 335, 289–294.
- Morita, K., Morita, S.H., 2002. Rule of age and size at maturity: individual variation in the maturation history of resident white-spotted charr. *J. Fish. Biol.* 61, 1230–1238.
- Nicholson, A.D., Jenkins, G., Sherwood, J., Longmore, A., 2008. Physical environmental conditions, spawning and early-life stages of an estuarine fish: climate change implications for recruitment in intermittently open estuaries. *Mar. Freshw. Res.* 59, 735–749.
- Norlem, M., Paraska, D., Hipsey, M.R., 2014. Sediment-water oxygen and nutrient fluxes in a hypoxic estuary. In: MODSIM2013 – 20th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, Adelaide, Australia, December 2013.
- Orr, P.T., Jones, G.J., Douglas, G.B., 2004. Response of cultured *Microcystis aeruginosa* from the Swan River, Australia, to elevated salt concentration and consequences for bloom and toxin management in estuaries. *Mar. Freshw. Res.* 55, 277–283.
- Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118, 1883–1891.
- Pichavant, K., Person-Le-Ruyet, J., Le Bayon, N., Sévère, A., Le Roux, A., Quémener, L., Maxime, V., Nonnotte, G., Boeuf, G., 2000. Effects of hypoxia on growth and metabolism of juvenile turbot. *Aquaculture* 188, 103–114.
- Pichavant, K., Person-Le-Ruyet, J., Le Bayon, N., Sévère, A., Le Roux, A., Quémener, L., Maxime, V., Nonnotte, G., Boeuf, G., 2001. Comparative effects of long-term hypoxia on growth, feeding, and oxygen consumption in juvenile turbot and European sea bass. *J. Fish. Physiol.* 59, 875–883.
- Pihl, L., Baden, S.P., Diaz, R.J., 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Mar. Biol.* 108, 349–360.
- Pihl, L., Baden, S.P., Diaz, R.J., Schaffner, L.C., 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacean. *Mar. Biol.* 112, 349–361.
- Potter, I.C., Hyndes, G.A., 1999. Characteristics of the ichthyofaunas of southwestern Australian estuaries, including comparisons with holarctic estuaries and estuaries elsewhere in temperate Australia: a review. *Aust. J. Ecol.* 24, 395–421.
- Potter, I.C., Beckley, L.E., Whitfield, A.K., Lenanton, R.C.J., 1990. Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environ. Biol. Fish.* 28, 143–178.
- Powers, S.P., Peterson, C.H., Christian, R.R., Sullivan, E., Powers, M.J., Bishop, M., Buzzelli, C.P., 2005. Effects of eutrophication on bottom habitat and prey resources of demersal fishes. *Mar. Ecol. Prog. Ser.* 302, 233–243.
- Prince, E.D., Goodyear, P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* 15, 451–464.
- R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (accessed February 2014).
- Roberts, J.J., Brandt, S.B., Fanslow, D., Ludsin, S.A., Potnoven, S.A., Scavia, D., Höök, T.O., 2011. Effects of hypoxia on consumption, growth, and RNA: DNA ratios of young yellow perch. *Trans. Am. Fish. Soc.* 140, 37–41.
- Robson, B.J., Hamilton, D.P., 2003. Summer flow event induces a cyanobacterial bloom in a seasonal Western Australian estuary. *Mar. Freshw. Res.* 54, 139–151.
- Robson, B.J., Bukaveckas, P.A., Hamilton, D.P., 2008. Modelling and mass balance assessments of nutrient retention in a seasonally-flowing estuary (Swan River Estuary, Western Australia). *Estuar. Coast. Shelf Sci.* 76, 282–292.
- Sakabe, R., Lyle, J.M., 2010. The influence of tidal cycles and freshwater inflow on the distribution and movement of an estuarine resident fish *Acanthopagrus butcheri*. *J. Fish. Biol.* 77, 643–660.
- Sarre, G.A., Potter, I.C., 1999. Comparisons between the reproductive biology of the black bream *Acanthopagrus butcheri* (Teleostei: Sparidae) in four estuaries with widely differing characteristics. *Int. J. Salt Lake Res.* 8, 179–210.
- Sarre, G.A., Potter, I.C., 2000. The age composition and growth rates of *Acanthopagrus butcheri* (Sparidae) vary among estuaries: some possible contributing factors. *Fish. Bull.* 98, 785–799.
- Sarre, G.A., Platell, M.E., Potter, I.C., 2000. Do the dietary compositions of *Acanthopagrus butcheri* in four estuaries and a coastal lake vary with body size and season and within and amongst these water bodies? *J. Fish. Biol.* 56, 103–122.
- Schelske, C.L., Odum, E.P., 1961. Mechanisms maintaining high productivity in Georgia estuaries. *Proc. Gulf Caribb. Fish. Inst.* 14, 75–80.
- Sharpe, D.M.T., Hendry, A.P., 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol. Appl.* 2, 260–275.
- Smith, K.A., 2006. Review of Fishery Resources and Status of Key Fishery Stocks in the Swan-canning Estuary. Fisheries Research Report No. 156. Department of Fisheries, Western Australia, p. 84.
- Smith, K., Howard, A., Brown, J., 2013. West coast nearshore and estuarine finfish resources status report. In: Fletcher, W.J., Santoro, K. (Eds.), Status Reports of the Fisheries and Aquatic Resources of Western Australia 2012–13: the State of the Fisheries. Department of Fisheries, Western Australia, pp. 71–88.
- Stahl, J.P., Kruse, G.H., 2008. Spatial and temporal variability in size at maturity of walleye pollock in the eastern Bering Sea. *Trans. Am. Fish. Soc.* 137, 1543–1557.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, p. 249.
- Stephens, R., Imberger, J., 1996. Dynamics of the Swan River Estuary: the seasonal variability. *Mar. Freshw. Res.* 47, 517–529.
- Surhone, L.M., Tennoe, M.T., Henssonow, S.F., 2010. OpenBUGS. Betascript Publishing, Mauritius, p. 108.
- Tesch, F.W., 1968. Age and growth. In: Ricker, W.E. (Ed.), *Methods for Assessment of Fish Production in Fresh Waters*. Blackwell Scientific Publications, Oxford, pp. 93–123.
- Thiel, R., Sepulveda, A., Kafemann, R., Nellen, W., 1995. Environmental factors as forces structuring the fish community of the Elbe Estuary. *J. Fish. Biol.* 46, 47–69.
- Thomson, C.E., Rose, T., Robb, M., 2001. Seasonal Water Quality Patterns in the Swan River Estuary, 1994–1998. technical report. Swan River Trust, Western Australia.
- Thronson, A., Quigg, A., 2008. Fifty years of fish kills in coastal Texas. *Estuar. Coasts* 31, 802–813.
- Twedley, J.R., Warwick, R.M., Clarke, K.R., Potter, I.C., 2014. Family-level AMBI is valid for use in the north-eastern Atlantic but not for assessing the health of microtidal Australian estuaries. *Estuar. Coast. Shelf Sci.* 141, 85–96.
- Twomey, L., John, J., 2001. Effects of rainfall and salt-wedge movement on phytoplankton succession in the Swan–Canning Estuary, Western Australia. *Hydrol. Process.* 15, 2655–2669.
- Tyler, R.M., Targett, T.E., 2007. Juvenile weakfish, *Cynoscion regalis*, distribution in relation to diel-cycling dissolved oxygen in an estuarine tributary. *Mar. Ecol. Prog. Ser.* 333, 257–269.
- Vaquier-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci.* 105, 15452–15457.
- Viney, N.R., Sivapalan, M., 2001. Modelling catchment processes in the Swan-Avon river basin. *Hydrol. Process.* 15, 2671–2685.
- Wannamaker, C.M., Rice, J.A., 2000. Effects of hypoxia on movements and behavior of selected estuarine organisms from the southeastern United States. *J. Exp. Mar. Biol. Ecol.* 249, 145–163.
- Western Australian Department of Water, 2014. River Monitoring Stations. Government of Western Australia. <http://kumina.water.wa.gov.au/waterinformation/wir/reports/publish/616011/g02.htm> (accessed 25.02.14).
- Whitfield, A.K., 1999. Ichthyofaunal assemblages in estuaries: a South African case study. *Rev. Fish. Biol. Fish.* 9, 151–186.
- Whittaker, R.H., Likens, G.E., 1975. The biosphere and man. In: Leith, H., Whittaker, R.H. (Eds.), *Primary Production of the Biosphere*. Springer-Verlag, New York, pp. 305–328.
- Williams, J., Hindell, J.S., Swearer, S.E., Jenkins, G.P., 2012. Influence of freshwater flows on the distribution of eggs and larvae of black bream *Acanthopagrus butcheri* within a drought-affected estuary. *J. Fish. Biol.* 80, 2281–2301.
- Williams, J., Jenkins, G.P., Hindell, J.S., Swearer, S.E., 2013. Linking environmental flows with the distribution of black bream *Acanthopagrus butcheri* eggs, larvae and prey in a drought affected estuary. *J. Fish. Biol.* 483, 273–287.
- Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. *Mar. Pollut. Bull.* 45, 35–45.
- Zammit, C., Sivapalan, M., Kelsey, P., Viney, N.R., 2005. Modelling the effects of land-use modifications to control nutrient loads from an agricultural catchment in Western Australia. *Ecol. Model.* 187, 60–70.