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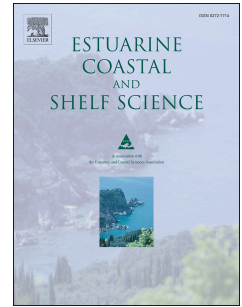
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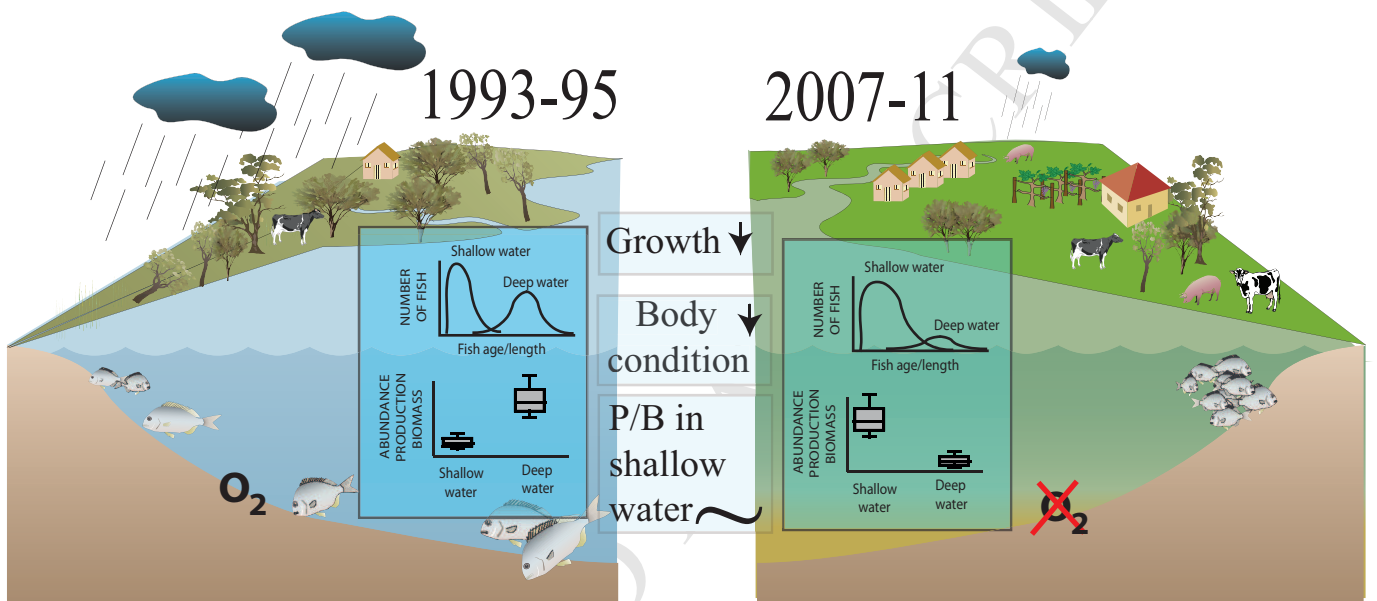
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Differential changes in production measures for an estuarine-resident sparid in deep and shallow waters following increases in hypoxia.

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ABSTRACT

This study determined how productivity measures for a fish species in different water depths of an estuary changed in response to the increase in hypoxia in deep waters, which had previously been shown to occur between 1993-95 and 2007-11. Annual data on length and age compositions, body mass, growth, abundance, biomass, production and production to biomass ratio (P/B) were thus determined for the estuarine-resident *Acanthopagrus butcheri* in nearshore shallow (<2 m) and offshore deep waters (2-6 m) of the upper Swan River Estuary in those two periods. Length and age compositions imply that the increase in hypoxia was accompanied by the distribution of the majority of the older and larger *A. butcheri* changing from deep to shallow waters, where the small fish typically reside. Annual densities, biomass and production in shallow waters of <0.02 fish m⁻², 2-4 g m⁻² and ~2 g m⁻² y⁻¹ in the earlier period were far lower than the 0.1-0.2 fish m⁻², 8-15 g m⁻² and 5-10 g m⁻² y⁻¹ in the later period, whereas the reverse trend occurred in deep waters, with values of 6-9 fish net⁻¹, 2,000-3,900 g net⁻¹, 900-1700 g net⁻¹ y⁻¹ in the earlier period vs <1.5 fish net⁻¹, ~110 g net⁻¹ and 27-45 g net⁻¹ y⁻¹ in the later period. Within the later period, and in contrast to the trends with annual abundance and biomass, the production in shallow waters was least during 2008/09, rather than greatest, reflecting the slow growth in that particularly cool year. The presence of substantial aggregations of both small and large fish in shallow waters accounts for the abundance, biomass and production in those waters increasing between those periods and thus, through a density-dependent effect, provide a basis for the overall reduction in growth. In marked contrast to the trends with the other three production measures, annual production to biomass ratios (P/B) in shallow waters in the two years in the earlier period, and in three of the four years of the later period, fell within the same range, i.e. 0.6-0.9 y⁻¹, but was only 0.2 y⁻¹ in 2008/09, reflecting the poor growth in that year. This emphasises the need to obtain data on P/B for a number of years when considering the implications of the typical P/B for a species in an estuary, in which environmental conditions and the growth of a species can fluctuate markedly between years.

Keywords: biomass; productivity; production to biomass ratio; inter-annual variations in growth; environmental degradation; density-dependence.

1.0 INTRODUCTION

The marked expansion of agriculture, urban and other developments in the catchments of estuaries during recent decades has led, through runoff from surrounding land, to increases in the amounts of nutrients and organic material in these systems (Lotze et al., 2006; Jennerjahn and Mitchell, 2013; Paerl et al., 2014). This has often resulted in a marked rise in primary production and thus of secondary production (Caddy, 1993, 2000; Maceina and Bayne, 2001; Powers et al., 2005). However, the accumulation of organic material, derived from autochthonous production, and often to an even greater extent from allochthonous sources (Elliott and Whitfield, 2011), results in increased microbial action in the benthic habitats of these systems (Wu, 2002; Baird et al., 2004; Powers et al., 2005). In the deep waters of microtidal estuaries, which are poorly flushed, microbial oxygen demand often exceeds replenishment rates and thus these waters tend to become hypoxic, particularly when the water column is stratified (Breitburg, 2002; Tweedley et al., 2016).

Work in the northern hemisphere has shown that, when the deep waters of estuaries become hypoxic, fish often tend to move to the better-oxygenated nearshore, shallow waters, thus leading to localised declines in the abundance of demersal fish in deep waters and increased densities of fish in nearshore refugia (Breitburg, 2002; Eby and Crowder, 2002; Eby et al., 2005; Craig, 2012; Campbell and Rice, 2014). Such habitat compression can lead to density-dependent effects, such as reductions in metabolic rate and growth (Eby et al., 2005; Breitburg et al., 2009; DeLong et al., 2014).

The production of fauna is defined as the “amount of tissue elaborated per unit time per unit area, regardless of its fate” (Clarke, 1946) and typically expressed as increase in biomass per unit of area and time, *e.g.* $\text{g m}^{-2} \text{y}^{-1}$ (Dolbeth et al., 2012). Since estimates of production combine data on abundance, biomass and growth, they provide a particularly useful measures of the ways in which environmental disturbances, such as those due to habitat modifications and the effects of climate change, influence fish populations and communities (Minns, 2009; Valentine-Rose et al., 2011). Although nutrient enrichment can lead to marked increases in the yield of key commercial fish species, as has occurred in the North Sea (Nixon & Buckley, 2002), extensive eutrophication and therefore marked increases in the extent of

hypoxia can result in localised declines in abundance, through causing mortality and emigration and implicitly reduced production in the directly-affected areas (Brietburg, 2002; Powers et al., 2005; Hughes et al., 2015). The relatively few studies of the production of fish species in an estuary have typically been based on marine taxa during their estuarine phase and, with estuarine residents, on small and short-lived species (Cowley and Whitfield, 2002; Pombo et al., 2007; Dolbeth et al., 2008) and there are no published data on how the production of a fish species changes following marked increases in hypoxia.

The ratios of production to biomass (P/B), i.e. the rates at which biomass is potentially changing (Randall and Minns, 2000), vary markedly among species. For example, the P/B for fish species, which inhabit the freshwater systems of eastern Canada, ranged widely from 0.12 y^{-1} for the Atlantic Salmon *Salmo salar* to 4.0 y^{-1} for the much smaller Blacknose Shiner *Notropis heterolepis* (Randall and Minns, 2000). Moreover, the annual P/Bs of species with short to medium longevity are likely to vary considerably among years, due to differences in age structure resulting from variations in recruitment and age-specific growth among years. Although the data of Dolbeth et al. (2010) demonstrate that the P/Bs of a range of fish species in estuaries can also range widely, none of those species was an estuarine resident, i.e. none completes its life cycle within its natal estuary.

The estuaries of south-western Australia are in a microtidal region in which rainfall and thus freshwater discharge are largely restricted to winter and early spring (Australian Bureau of Meteorology, 2017; Western Australian Department of Water, 2017). These estuaries, such as the Swan River Estuary, are thus poorly flushed, particularly during the dry summer and autumn, and consequently large amounts of nutrients and organic material become retained in their deeper waters (Cottingham et al., 2014; Tweedley et al., 2014). Between the early 1990s and about 2010, the extent of such accumulations increased in deeper waters, largely due to declines in rainfall and thus a reduction in flushing, thereby leading to an increase in eutrophication and the extent of hypoxia in deeper waters (Cottingham et al., 2014). Indeed, Cloern et al. (2014) found the Swan River Estuary to be the second most hypertrophic of the 131 estuarine coastal ecosystems worldwide for which they had collated data.

The Black Bream *Acanthopagrus butcheri*, which can attain total lengths of 500 mm and live for up to 30 years (Morison et al., 1998; Potter et al., 2008), is among the most important recreational and commercial finfish species in the estuaries of southern Australia (Lenanton and Potter, 1987; Jenkins et al., 2010; Cottingham et al., 2015). Because this sparid completes its life cycle within its natal estuary, it is exposed, throughout life, to the effects of any deleterious changes in its environment (Cottingham et al., 2014; Valesini et al., 2017). Sparids, such as *A. butcheri*, have a remarkable ability to respond to changes in their environment (Chuwen et al., 2007; Gardner et al., 2013; Doubleday et al., 2015; Wakefield et al., 2015). This is reflected in the finding that, although the extent of hypoxia has been shown to increase in the Swan River Estuary as freshwater discharge declined, *A. butcheri* continued to be represented by a substantial population (Cottingham et al., 2014). However, the growth, body condition and length at maturity declined and age at maturity increased, which represent the types of response that would be expected by a species with 'plastic' biological characteristics (Cottingham et al., 2014). Furthermore, the trends in catches imply that, as the extent of hypoxia in deep waters increased, the *A. butcheri* that would typically have occupied the deep waters tend to remain in the better oxygenated shallow waters. The resultant greatly increased density of this species in the nearshore, shallow environment would, in turn, help account for the overall reduction in growth.

This study has determined the extent to which annual abundance, biomass and production, and thus P/B, of *A. butcheri* in the shallow and deep waters of the Swan River Estuary changed between 1993-95 and 2007-11 as the growth and body condition of this sparid declined following marked increases in hypoxia in the deeper waters (Cottingham et al., 2014). Initially, the length and age compositions in shallow and deep waters in the two periods were analysed. The results were used to explore the hypothesis that the increase in density of *A. butcheri* in shallow waters was related to many older and larger fish tending to occupy the better oxygenated shallow waters, rather than the deep waters they would have typically occupied under less hypoxic conditions. The data were next used to determine the extents to which the decreases in abundance in deep water and increases in shallow water were accompanied by changes in biomass in those waters and to elucidate the extent of inter-annual variations

within each period. As the growth of *A. butcheri* had been shown previously to vary conspicuously between years (Cottingham et al., 2016), the annual productions and P/Bs were calculated to elucidate the extent to which they were influenced by age-specific growth between and within periods. The implications of the trends exhibited by the above production measures for fish species that inhabit estuaries are discussed.

2.0 MATERIALS AND METHODS

2.1 Sampling regime

Acanthopagrus butcheri was sampled in nearshore, shallow (<2 m deep) and offshore, deep waters (2-6 m deep) of the upper region of the Swan River Estuary (Fig. 1), where this sparid typically resides for most of the year (Sarre and Potter, 1999, 2000; Cottingham et al., 2014). Although some *A. butcheri* are flushed downstream during winter, when freshwater discharge increases markedly as a result of the highly seasonal rainfall, they move back in spring to the upper estuary where they spawn. The data for *A. butcheri* in winter are thus not included in the analyses. Shallow water was sampled by seine and deep water by gill nets.

Shallow and deep water were both sampled monthly between the austral spring of 1993 and austral autumn of 1995, thus representing the two ‘years’ comprising 1993/94 and 1994/95 (Sarre and Potter, 2000). Shallow waters were later sampled seasonally between spring 2007 and autumn 2011, thus representing the four ‘years’ comprising 2007/08, 2008/09, 2009/10 and 2010/11 (Cottingham et al., 2014). Deep waters were also sampled between spring and autumn in 2007/08 and 2008/09, but not subsequently as few *A. butcheri* were being caught. Note that independent sampling in deep waters in recent years has also yielded few *A. butcheri* (Hallett, 2016). As *A. butcheri* spawns in spring (Cottingham et al., 2014), the individuals in each age class in each of the above ‘years’ encompassed the full range from youngest to oldest fish within that age class. The 1993/94 and 1994/95 years are subsequently referred to collectively as the “earlier period” and those between 2007/08 and 2010/11 as the “later period”.

Shallow water was sampled during the day at six sites (Fig. 1) using a 41.5 m seine, which contained a 1.5 m wide bunt made of 9 mm mesh and two 20 m long wings comprising 25 mm mesh. This seine, which swept an area of 274 m², was deployed in a semi-circle from the bank, using a small boat, and then hauled on to the shore. Deep water was sampled at nine sites using sunken composite gill nets, with six of these each located offshore from a seine sampling site. The gill net consisted of eight 20 m long and 2 m high panels, each with a different stretched mesh size of either 38, 51, 63, 76, 89, 102, 115 or 127 mm. It was set parallel to the shore in water depths of 2-6 m, just after sunset, and retrieved 3 h later.

Following their capture, *A. butcheri* were euthanised in an ice slurry and transported to the laboratory, where they were sexed and their total length (TL) and mass recorded to the nearest 1 mm and 0.1 g, respectively. The growth zones in the otoliths of each *A. butcheri*, which had previously been shown to be formed annually in this species (Sarre and Potter, 2000), were counted and used for ageing that fish. Full details of the ageing procedures are given in Sarre and Potter (2000) and Cottingham et al. (2014). von Bertalanffy growth curves were constructed for females and males of *A. butcheri* in the Swan River Estuary using lengths at age, previously determined for each sex in 1993-95 (Sarre and Potter, 2000) and in 2007-11 (Cottingham et al., 2014). A likelihood-ratio test was used to determine whether the growth curves of each sex differed significantly between those two periods (see Cottingham et al. (2014) for further details).

2.2 Densities in shallow waters and catch rates in deep waters

Annual indices of abundance of *A. butcheri* in shallow and deep waters were calculated from the seine and gill net catches in each of the three seasons sampled in a year and expressed as fish m⁻² and fish net⁻¹ h⁻¹, respectively. However, as the seine and gill net catches of *A. butcheri* were highly skewed and often zero in seine catches in 1993-95 and in gill net catches in 2007-09, the catches in shallow and deep waters were assumed to conform to delta log-normal distributions (Pennington, 1996). Thus, the number of samples containing *A. butcheri* in each season at each depth was assumed to have a binomial distribution,

whereas the number of fish in each of those samples that contain *A. butcheri* in that seasonal sample was assumed to have a log-normal distribution. The mean and standard deviation for the log-normal distribution for each season, year and depth category were derived from a GLM analysis relating the natural logarithms of the catches containing *A. butcheri* to season and year.

Uncertainty of the annual abundance estimates was explored by calculating (boot-strapped estimates of) densities and catch rates using 1000 parametrically-resampled (Haddon, 2011; Efron, 2012) sets of number of fish caught in each season. First, for each water depth, a random number, representing the number of catches containing *A. butcheri* for a given season, was drawn from the binomial distribution, in which the probability of a catch containing *A. butcheri* was set equal to the observed proportion of catches containing *A. butcheri*. Second, for each catch containing *A. butcheri* within each season and year, a random number, representing the number of fish caught, was drawn from the log-normal distribution of such catches for that season derived from the GLM analysis. All analyses employed R (R Core Team, 2016).

2.3 Annual biomass, production and P/B

The boot-strapped catches determined when estimating annual abundances and their uncertainties were also employed when calculating estimates of biomass and production. For this, each fish in each catch containing *A. butcheri* in each of the above 1000 random seasonal samples for each year in shallow and deep waters, was assigned a random age, which was drawn by resampling, with replacement, *i.e.* boot strapping, from the age composition for the corresponding season and year. The estimated length of each fish (at its age of capture) was calculated from its resampled age, using the year-effects growth model fitted to the lengths at age of *A. butcheri* in the Swan River Estuary for the years encompassing the present study (Cottingham et al., 2016; see also brief summary in Supplementary Materials). For this calculation of expected length at age, each of the 1000 samples for each season was paired with a random set of year-specific growth parameter estimates, *i.e.* asymptotic lengths and von Bertalanffy growth coefficients, which had been obtained by boot strapping in that growth study.

The body mass and instantaneous rate of increase in body mass of each fish in the samples for each season and year employed estimates of its expected mass and a forward difference approximation of the derivative of expected mass at age, calculated using the year effects growth model (Cottingham et al., 2016). The mass of each fish was back-transformed, with bias correction (Beauchamp and Olson, 1973), from the value predicted by linear regression of the natural logarithms of mass vs length for *A. butcheri* in its year of capture.

The total biomass for resampled fish in shallow and deep waters in each year was calculated by summing the estimated body masses of the fish in each random seasonal sample for that year. Production was calculated using the ‘instantaneous growth method’ (Waters, 1977), *i.e.* by summing the instantaneous increases in body masses of those fish in the corresponding seasonal samples for that year. For each of the 1000 samples in each year, indices of annual biomass and production in shallow and deep waters were then calculated by dividing the totals for biomass and instantaneous rates of change by the corresponding sampling effort in that year. The biomass and production in shallow waters were thus expressed as g m^{-2} and $\text{g m}^{-2} \text{y}^{-1}$, respectively, and, in deep waters, as g net^{-1} and $\text{g net}^{-1} \text{y}^{-1}$, respectively.

Annual estimates of production to biomass ratio (P/B y^{-1}) in shallow and deep waters were calculated for each of the 1000 boot-strapped samples by dividing the production for that year by its biomass.

As the above calculations of production combine the effects of growth and abundance over size and age classes, the instantaneous rates of increase in the mass of fish, with an initial TL of 115 mm, from different years, were calculated to provide a length-standardised description of the effect of changes in growth and body condition among years for a specific size class. This was achieved using the boot-strapped growth parameters derived for the year-effects growth model (Cottingham et al., 2016), combined with the annual mass-length relationships. The initial length of 115 mm approximates the length of *A. butcheri* at the beginning of the second year of life (Cottingham et al., 2016).

2.4 Comparisons among years and periods

The 1,000 point estimates for abundance, biomass, production and P/B in each year were compared with the corresponding point estimates in each of the other years. The values in the different years for each variable were considered to differ significantly at the 0.05, 0.01 and 0.001 levels if the number of comparisons, in which the first value was less than the second was ≤ 25 or ≥ 975 , ≤ 5 or ≥ 995 , and 0 or 1, respectively. For biomass, production and P/B, the point estimates for each bootstrapped sample for each year were calculated using the parameters derived from fitting the year-effect growth model. The above analytical approach thus acknowledges the inter-dependence of growth among years. It was also applied when analysing the increase in mass in the different years.

3.0 RESULTS

3.1 Length and age-frequency distributions and overall growth

The TLs of *A. butcheri* caught in 1993/94 by seine in shallow waters ranged from 67 to 402 mm, with the majority between 70 and 149 mm, within which they produced a broad mode at 100-129 mm (Fig. 2). In contrast, the TLs of *A. butcheri* caught in that year by the composite gill net in deep waters ranged from 104 to 439, and produced a unimodal distribution with fish being most abundant in the length classes between 230 and 289 mm. The length distributions for the shallow and deep water samples in 1994/95 had essentially both shifted to the right of those for the preceding year (Fig. 2).

The TLs of *A. butcheri* caught by seine in shallow waters in each of the four years between 2007/08 and 2010/11 represented the same wide range of ~40-349 mm, with the distribution in 2007/08 producing a broad mode at 130-179 mm (Fig. 2). While few fish with lengths <120 mm were caught in the shallows in 2007/08, such fish were abundant in catches in these waters in 2008/09, 2009/10 and 2010/11. Substantial numbers of fish with TLs >120 mm were caught in the shallows in each year between 2007/08 and 2010/11, producing well defined peaks at 139 to 179 mm in the first of those years and at 170-199 mm in the second of those years.

Sampling the same gill net sites in 2007/08 and 2008/09 as in 1993/94 and 1994/95, yielded few *A. butcheri* (Fig. 2) and, thus, gill netting was not continued after 2008/09 (Cottingham et al., 2014).

Although the majority of *A. butcheri* caught in 1993/94 and 1994/95 were less than 5 years old, those <2 years old were obtained predominantly by seining in nearshore, shallows, whereas those greater than this age were taken very largely by gill netting in offshore, deep waters (Fig. 2). In contrast to the situation with seining in the above two years, this sampling method in 2007/08 to 2010/11 yielded substantial numbers of 3+ and 4+ fish, as well as younger fish and, in some years, appreciable numbers of 5+ or older fish. The fish caught in deep water in 2007/08 and 2008/09 belonged collectively to age classes ranging from 1+ to 4+ and were in such small numbers that they are only just detectable as a thickening at the tops of the bars for their respective age classes (Fig. 2).

A likelihood-ratio test demonstrated that, on the basis of the von Bertalanffy curves for females and males of *A. butcheri*, the growth of both sexes was far greater in 1993-95 than 2007-11 (both $P < 0.001$, in Cottingham et al., 2014). This difference in growth between the two periods is reflected in the females and males of *A. butcheri* typically requiring three further years to attain 250 mm, the minimum legal length for retention of this species (Fig. 3).

3.2 Abundance, biomass, production and P/B

Median estimates of abundance of *A. butcheri* in shallow waters were < 0.02 fish m^{-2} in both 1993/94 and 1994/95 and thus far less than in any year between 2007/08 and 2010/11, for which they ranged from 0.1 to 0.2 fish m^{-2} (Fig. 4a). These trends were paralleled by the median estimates of biomass in shallow waters, with the values of < 4 g m^{-2} in both 1993/94 and 1994/95 markedly less than in any year between 2007/08 to 2010/11, among which values ranged from 8 to 15 g m^{-2} (Fig. 4b). Likewise, the median production of 1.7 and 2.0 g $m^{-2} y^{-1}$ for *A. butcheri* in shallow waters in 1993/94 and 1994/95, respectively, lie below the range of 2.8 to 9.7 g $m^{-2} y^{-1}$ for the four years between 2007/08 and 2010/11 (Fig. 4c).

In striking contrast to the situation in shallow waters in the two periods, the abundance, biomass and production in deep waters were each far greater in the earlier than later periods (Fig. 4d, e, f). Thus, for example, the median estimates of 872 and 1719 g $net^{-1} y^{-1}$ for production in deep waters in 1993/94

and 1994/95, respectively, greatly exceeded the corresponding values of only 36 and 22 g net⁻¹ y⁻¹ in 2007/08 and 2008/09, respectively (Fig. 4f).

The abundance, biomass and production in shallow waters in 1993/94 did not differ significantly from the values for the corresponding variable in 1994/95 ($P>0.05$) and the same lack of a significant difference applied to those three variables in the four years between 2007/08 and 2010/11 ($P>0.05$). However, the abundance and biomass in shallow waters in 1993/94 and 1994/95 did differ significantly from the corresponding and greater values for each year from 2007/08 to 2010/11 ($P<0.01$ or <0.001). The same was true for production in all inter-annual comparisons except for 1993/94 and 1994/95 vs 2008/09 ($P>0.05$), recognising, however, that the value for production in the first two of those years was still less than that for 2008/09.

As with shallow waters, the values for abundance, biomass and production in deep waters in 1993/94 did not differ significantly from those for their corresponding variable in 1994/95 and the same lack of a significant difference was true for those variables in 2007/08 vs 2008/09 ($P>0.05$). The values for these three biotic variables in the two years in the earlier period were significantly different, however, from those for the corresponding variables in the two years in the later period ($P<0.05$ to <0.001).

In shallow waters, the median P/B in 1993/94 and 1994/95, and in each of the four years between 2007/08 and 2010/11, ranged from ~0.6 to 0.8 y⁻¹, except in 2008/09 when it was far lower, *i.e.* 0.2 y⁻¹ (Fig. 4g). In deep waters, the median P/Bs in 1993/94 and 1994/95 were both ~0.45 y⁻¹ (Fig. 4h). However, as the abundance, biomass and production were each very low in deep waters in 2007/08 and 2008/09, it was considered inappropriate to place emphasis on calculations for P/Bs for those years.

The overall median values of 95 g y⁻¹ in 1993/94 and 125 g y⁻¹ in 1994/95 for the instantaneous rate of increase in mass by *A. butcheri*, with an initial length of 115 mm, far exceeded those for the four years between 2007/08 and 2010/11, which ranged from 25 to 60 g y⁻¹ (Fig. 5).

4.0 DISCUSSION

This study provides the first detailed analyses of the extents to which the length and age compositions, abundances (densities or catch rates), biomass, production and P/B of a fish species in the shallow and deep waters of an estuary changed after its environment had undergone pronounced deleterious changes. The data derived for those variables for the sparid *Acanthopagrus butcheri* in the microtidal Swan River Estuary are considered against the background of the pronounced increase that, between 1993-95 and 2007-11, had been demonstrated statistically to occur in the extent of hypoxia in the deep waters of the region in which this species typically resides (Cottingham et al., 2014). As pointed out in the introduction, the changes shown to have taken place between these two periods in the biological characteristics of *A. butcheri* such as growth, body condition and distribution within the estuary are consistent with the recorded responses of fishes to hypoxia elsewhere (cf Thiel et al., 1995; Pichavant et al., 2000, 2001; Eby et al., 2005; Cottingham et al., 2014). Moreover, the reduction in the length at maturity and increase in age at maturity of *A. butcheri* in the Swan River Estuary between the two periods are also consistent with the trends that would be anticipated with declines in growth associated with deleterious environmental changes (Stearns, 1992).

4.1 Length and age-frequency distributions

Length-frequency distributions clearly demonstrate that, in 1993-95, small fish dominated the catches in shallow waters and large fish those in deep waters, whereas, in 2007-11, the catches in shallow waters contained substantial numbers of fish encompassing a wide range of lengths, with few fish caught in deep waters. The proportion of larger fish in the samples obtained collectively by seine and gill netting in 1993/94 and in 1994/95 was conspicuously far greater than in those obtained by those same methods in 2007/08 and 2008/09, the two years in which gill netting was conducted in the later period. From the lengths at age in von Bertalanffy growth curves, these differences can be largely attributed to greater overall growth in the earlier than later period (Fig. 3).

The trends exhibited by the length-frequency distributions in seine samples reflect differences in age compositions. Thus, the latter distributions emphasise that the *A. butcheri* in shallow waters of the

Swan River Estuary in the earlier period consisted predominantly of fish in their first two years of life, whereas those in the later period contained substantial numbers of a wide range of age classes. In contrast, while fish of two years in age and older were relatively abundant in deep waters in the earlier period, few fish of any age were present in those waters in 2007/08 and 2008/09, after which gill netting was discontinued. As gill netting in another study in 2012-16 still yielded low numbers of *A. butcheri* in the upper Swan River Estuary, the abundance of this species in deep water continued to remain low (Hallett, 2016).

4.2 Abundance, biomass and production

As shallow waters were sampled by seine and deep waters by gill net, the estimates of abundance, biomass and production in those two habitats cannot be directly compared. It is appropriate, however, to compare the values, in 1993-95 and 2007-11, for each of those biotic variables within shallow and deep waters separately and then to compare the resultant inter-period trends in each water depth.

Abundances of *A. butcheri* in shallow and deep waters of the upper Swan River Estuary in 1993/94 and 1994/95 both differed markedly from those in the four years between 2007/08 and 2010/11. More specifically, the median values in deep waters were far greater in the earlier than later period, whereas precisely the opposite trend occurred in shallow waters. These trends parallel those of mean densities, derived previously using the same base data for those waters, but which employed only year, rather than both year and season, as a fixed factor in the GLM (Cottingham et al., 2014).

The above marked inter-period differences between the trends exhibited by the length and age compositions and relative abundances in nearshore, shallow waters and those in offshore, deep waters clearly imply the following. As the deep waters of the Swan River Estuary became increasingly hypoxic as freshwater discharge declined, the larger and older *A. butcheri* showed a very pronounced tendency to occupy the better oxygenated shallow waters. The shift in distribution of the older and larger fish from offshore, deep to nearshore, shallow waters, where the younger and smaller fish still reside, accounts for the marked increase in densities in nearshore waters. Likewise, the Spot *Leiostomus xanthurus*, Atlantic

Croaker *Micropogonias undulatus*, Hogchoker *Trinectes maculatus* and juvenile Weakfish *Cynoscion regalis* also congregate in the better oxygenated shallow waters of other estuaries when the deeper waters become hypoxic (Pihl et al., 1991; Tyler and Targett, 2007; Campbell and Rice, 2014).

As with densities, the biomass and production in shallow waters in each of the four years between 2007/08 and 2010/11 exceeded those in 1993/94 and 1994/95, which was reflected in overall inter-period increases of three to four times in both biomass and production. The trends exhibited by the median values for production in those waters in the later period did not track, however, those of density and biomass. Thus, the samples in 2008/09 yielded the greatest densities and biomass, but the lowest production, which, from data derived from the year-effect growth model (Fig. 5), was attributable to particularly slow growth in that year, which, in turn was related to the especially low temperatures (Cottingham et al., 2016).

The very marked decline that occurred in the biomass and production in deep waters, between the earlier period (1993/94 and 1994/95) and the two years sampled in the later period (2007/08 and 2008/09) was even more pronounced than that of catch rates. Indeed, biomass and production fell precipitously by over 30 times between those two periods.

4.3 P/B

Although growth in the later period, 2007-11, was less than in the earlier period, 1993-95, the ranges in the values for annual P/Bs in nearshore, shallow waters in the two periods were similar, i.e. ~ 0.6 to 0.9 y^{-1} , except in 2008/09, when it was far lower, i.e. $\sim 0.2 \text{ y}^{-1}$. This broad comparability of P/Bs in all years, apart from 2008/09, reflects the strong influence on the P/B of the relatively smaller numbers and faster growth in the earlier period being offset by the marked effect of the presence, in the later period, of relatively greater numbers of small fish, which grow faster than larger fish. The slower growth of fish in the later period is demonstrated by the growth of fish of a standard size being slower in that period than the earlier period, both in terms of mass (Fig. 5) as well as length (Cottingham et al., 2016). The far lower P/B of fish in 2008/09 reflects the poor growth of *A. butcheri* in that particularly cool year (Cottingham et

al., 2016). The fact that the very similar P/Bs of just over 0.4 y^{-1} in deep waters in 1993/94 and 1994/95 were less than those in shallow waters in all years of both periods, except 2008/09, presumably reflects the presence, in deeper waters during the earlier period, of relatively greater numbers of large fish, which grow slower than small fish.

As *A. butcheri* typically require three additional years to attain the MLL of 250 mm, the proportion of legal-sized fish within the population will have declined. Although P/B in the shallows has typically remained relatively stable over most years, the proportion of P/B associated with legal-sized fish, which reflects the proportion of production available to fishers, is markedly reduced.

4.4 Comparisons with other estuarine studies

As a range of different types of method have been employed for catching fish in estuaries, it is crucial to recognise that estimates of the abundances and biomass of species, and hence their production and P/B can differ markedly among studies according to fishing mode (Whitfield, 2016). The fishing method may be active or passive and, when using nets, employ gear with different dimensions and mesh sizes and consequently have different selectivities. While, in broad terms, the catches obtained using active fishing methods, e.g. seining and otter trawling, yield densities in terms of area sampled, those derived from passive techniques, such as gill netting and trapping, typically provide catch rates in terms of time sampled. Thus, when sampling technique varies, caution has to be exercised when making direct comparisons of production measures for a species or among species. Furthermore, and in contrast to *A. butcheri*, most of the longer-lived fish species found in estuaries are typically marine and present for a restricted period and predominantly as juveniles (Potter et al., 2015). Consequently, comparisons between the relative abundances, biomass, production and P/B of those species with those of *A. butcheri* will often not be based on a complete range of their sizes and life-cycle stages.

As with *A. butcheri* in the Swan River Estuary and many other estuaries in southern Australia (Loneragan and Potter, 1990; Sarre and Potter, 2000; Jenkins et al., 2010; Williams et al., 2012), another sparid, *Rhabdosargus holubi*, makes a very substantial contribution to the ichthyofauna in temperate

estuaries of southern Africa (James et al., 2007). In one of those estuaries, the East Kleinemonde, the biomass and production of *R. holubi*, derived from data from seining throughout this very short estuary, was 16.1 g m^{-2} and $41.4 \text{ g m}^{-2} \text{ y}^{-1}$, respectively (Cowley and Whitfield, 2002). These values exceed the corresponding annual values, derived for *A. butcheri* by seining throughout the far longer length of the upper Swan River Estuary, i.e. 1.5 g m^{-2} and $2 \text{ g m}^{-2} \text{ y}^{-1}$ in 1993/94 and 2 g m^{-2} in and $3.5 \text{ g m}^{-2} \text{ y}^{-1}$ in 1994/95 and the $10\text{-}12.5 \text{ g m}^{-2}$ and $2.5\text{-}7 \text{ g m}^{-2} \text{ y}^{-1}$, respectively, for the four years between 2007/08 and 2010/11. The exceptional value for production by *R. holubi* is reflected in this species contributing as much as 74% to total fish production in the East Kleinemonde Estuary (Cowley and Whitfield, 2002). It is reiterated, however, that, unlike *A. butcheri*, which is confined to estuaries for the whole of its life cycle, *R. holubi* is a marine species that uses estuaries predominantly as a nursery area (Cowley and Whitfield, 2002) and thus the above estimates for *R. holubi* are restricted, by necessity, to young and relatively fast-growing fish.

The values derived for biomass and production in the East Kleinemonde Estuary for the 13 marine species (other than *R. holubi*), which, like *R. holubi* and *A. butcheri*, are relatively long-lived, ranged from 0.002 to 2.2 g m^{-2} and 0.012 to $3.3 \text{ g m}^{-2} \text{ y}^{-1}$, respectively. They were thus far lower than those for *R. holubi*, with the upper end of their range approximating those of *A. butcheri* in 1993/94 and 1994/95, but typically less than those of *A. butcheri* in the four years in 2007-11. In the Embley Estuary in tropical Australia, the biomass of 1.3 g m^{-2} , determined from seine data for the sparid *Acanthopagrus berda*, which spawns in or near the estuary mouth with its eggs transported out to sea (Garratt, 1993), was substantially less than for *A. butcheri* (Blaber et al., 1989). This implies that the density of this similarly-sized sparid in this estuary is less than those of *A. butcheri* and also *R. holubi* in the above estuaries. The biomass and production values for *A. butcheri* exceeded those for each of the five species studied by Dolbeth et al. (2010) in two Portuguese estuaries.

The P/B of 2.6 y^{-1} , calculated for the assemblage of *R. holubi* in the East Kleinemonde Estuary, using the production and biomass values in Cowley and Whitfield (2002), is far greater than the $\sim 0.2\text{-}0.9 \text{ y}^{-1}$, derived for *A. butcheri* from data across its life cycle. Similarly, the P/Bs were substantially greater

for the marine species *Dicentrarchus labrax* and *Platichthys flesus* in the Minho and Mondego estuaries in Portugal than for *A. butcheri*, with values ranging from as low as 1.3 to as high as 6.9 y^{-1} (Dolbeth et al., 2010). Furthermore, the P/Bs for *Solea solea* ranged from 1.6 to 3.9 y^{-1} when the first two age classes were present in an estuary, and from 5.4 to 11.6 y^{-1} when only the first age class was present (Dolbeth et al., 2010). The far greater values, when data are restricted to just 0+ fish, reflects the more rapid growth and lower body mass of the youngest fish and emphasises the extreme caution when drawing conclusions from comparisons between the P/B values for marine species that essentially use that estuary as a nursery areas and those of estuarine residents. Furthermore, it is reiterated that, among the P/Bs for the six years for *A. butcheri* in shallow waters, the value for one year, 2008/09, was far lower than in each of the other years reflecting the slow growth in that year.

4.4 Conclusions

In summary, this unique study has integrated data for the length and age compositions, abundance, growth and body condition of an estuarine fish species of moderate longevity in the nearshore, shallow and offshore, deep waters of an estuary in two periods (1993/94 and 1994/95, and 2007/08 to 2010/11), between which the deep waters of that system became far more hypoxic. As hypothesised, the abundance, biomass and production of *A. butcheri* increased markedly in shallow waters and declined precipitously in deep waters. Comparisons of the length and age compositions imply that, between the two periods, the older and larger fish showed a far greater tendency to occupy the shallows, where the smaller fish live. The increased density in those shallow waters would help account for the decline in growth between those periods. Although, in the later period, abundance and biomass in shallow waters rose to a maximum in 2008/09, production fell to a minimum in that year, as a result of particularly slow growth. That slow growth also accounts for the P/B in shallow water in 2008/09 declining to $\sim 0.2 y^{-1}$, a value far less than those in the range of $\sim 0.6-0.9 y^{-1}$ for the other three years in the later period and the two years in the earlier period. The markedly lower P/B in the shallow waters in one year emphasises that it is important to obtain values for at least a few years when basing generalisations on this production measure for a

species in an estuary, in which environmental conditions and the growth of species can vary naturally and markedly between years. Furthermore, such marked environmental variations inevitably lead to pronounced variations in annual recruitment, as has been shown to occur in *A. butcheri* (Morison et al., 1998; Cottingham et al., 2015) and this can also influence the P/B. The proportion of legal-sized fish in the population and their contribution to P/B declined markedly between 1993-95 and 2007-11.

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REFERENCES

- Australian Bureau of Meteorology, 2017. Climate Data Online. Location: Perth Airport. <http://www.bom.gov.au/climate/data/?ref¼ftr>. Accessed 01.01.17.
- Baird, D., Christian, R.R., Peterson, C.H., Johnson, G.A., 2004. Consequences of hypoxia on estuarine food web and ecosystems function: energy diversion from consumers to microbes. *Ecol. Appl.* 14, 805-822.
- Beauchamp, J.J., Olson, J.S., 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology* 54, 1403-1407.
- Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1989. Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuar. Coast. Shelf Sci.* 29, 509-531.
- Breitburg, D.L., 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25, 767-781.
- Breitburg, D.L., Hondorp, D.W., Davias, L.A., Diaz, R.J., 2009. Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. *Ann. Rev. Mar. Sci.* 1, 329-349.

- Caddy, J.F., 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Rev. Fish. Sci.* 1, 57-95.
- Caddy, J.F., 2000. Marine catchment basin versus impacts of fisheries on semi-enclosed seas. *ICES J. Mar. Sci.* 57, 628-640.
- Campbell, L.A., Rice, J.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, 119-213.
- 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. *Biol. Fish.* 80, 363-376.
- Clarke, G.L., 1946. Dynamics of production in a marine area. *Ecol. Monogr.* 16, 321-355.
- Cloern, J.E., Foster, S.Q., Kleckner, A.E., 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. *Biogeosciences* 11, 2477-2501.
- Cottingham, A., Hall, N.G., Potter, I.C., 2015. Performance and contribution to commercial catches and egg production by restocked *Acanthopagrus butcheri* (Sparidae) in an estuary. *Estuar. Coast. Shelf Sci.* 164, 194-203.
- Cottingham, A., Hesp, S.A., Hall, N.G., Hipsey, M.R., Potter, I.C., 2014. Marked deleterious changes in the condition, growth and maturity schedules of *Acanthopagrus butcheri* (Sparidae) in an estuary reflect environmental degradation. *Estuar. Coast. Shelf Sci.* 149, 109-119.
- Cottingham, A., Hall, N.G., Potter, I.C., 2016. Factors influencing growth of *Acanthopagrus butcheri* (Sparidae) in a eutrophic estuary have changed over time. *Estuar. Coast. Shelf Sci.* 168, 29-39.
- Cowley, P.D., Whitfield, A.K., 2002. Biomass and production estimates of a fish community in a small South African estuary. *J. Fish Biol.* 61, 74-89.
- 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.
- DeLong, J.P., Torrance, C.H., Vasseur, D.A., 2014. Competition and the density dependence of metabolic rates. *J. Anim. Ecol.* 83, 51-58.
- Dolbeth, M., Cusson, M., Sousa, R., Pardal, M.A., 2012. Secondary production as a tool for better understanding of aquatic ecosystems. *Can. J. Fish. Aquat. Sci.* 69, 1230-1253.
- Dolbeth, M., Martinho, F., Freitas, V., Costa-Dias, S., Campos, J., Pardal, M.Â., 2010. Multi-year comparisons of fish recruitment, growth and production in two drought-affected Iberian estuaries. *Mar. Freshwat. Res.* 61, 1399-1415.
- Dolbeth, M., Martinho, F., Viegas, I., Cabral, H., Pardal, M.A., 2008. Estuarine production of resident and nursery fish species: Conditioning by drought events? *Estuar. Coast. Shelf Sci.* 78, 51-60.
- Doubleday, Z.A., Izzo, C., Haddy, J.A., Lyle, J.M., Ye, Q., Gillanders, B.M., 2015. Longterm patterns in estuarine fish growth across two climatically divergent regions. *Oecologia.* 179, 1079-90.

- 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.
- Efron, B., 2012. Bayesian inference and the parametric bootstrap. *The Annals Appl. Stat.* 6, 1971-1997.
- Elliott, M., Whitfield, A.K., 2011. Challenging paradigms in estuarine ecology and management. *Estuar. Coast. Shelf Sci.* 94, 306-314.
- Gardner, M.J., Cottingham, A., Chaplin, J.A., Hesp, S.A., Jenkins, G.I., Phillips, N.M., Potter, I.C., 2013. Comparisons of the biological and genetic characteristics of restocked and wild individuals of a sparid (*Acanthopagrus butcheri*) in an estuary. *Rev. Fish. Sci.* 21, 441-452.
- Garratt, P.A., 1993. Spawning of riverbream, *Acanthopagrus berda*, in Kosi estuary, S. Afr. *J. Zool.* 28, 26-31.
- Haddon, M., 2011. *Modelling and Quantitative Methods in Fisheries*, Second Edition. Boca Raton, CRC Press.
- Hallett, C.S., 2016. Assessment of the condition of the Swan Canning Estuary in 2016, based on the Fish Community Index of estuarine condition. Final report to the Department of Parks and Wildlife. Murdoch University, Western Australia, 35 pp.
- Hughes, B.B., Levey, M.D., Fountain, M.C., Carlisle, A.B., Chavez, F.P., Gleason, M.G., 2015. Climate mediates hypoxic stress on fish diversity and nursery function at the land–sea interface. *Proc. Natl Acad. Sci.* 112, 8025-8030.
- James, N.C., Cowley, P.D., Whitfield, A.K., Lamberth, S.J., 2007. Fish communities in temporarily open/closed estuaries from the warm- and cool-temperate regions of South Africa: A review. *Rev. Fish Biol. Fish.* 17, 565-580.
- Jenkins, G.P., Conron, S.D., Morison, A.K., 2010. Highly variable recruitment in an estuarine fish is determined by salinity stratification and freshwater flow: implications of a changing climate. *Mar. Ecol. Prog. Ser.* 417, 246-261.
- Jennerjahn, T.C., Mitchell, S.B., 2013. Pressures, stresses, shocks and trends in estuarine ecosystems – an introduction and synthesis. *Estuar. Coast. Shelf Sci.* 130, 1–8.
- Lenanton, R.C.J., Potter, I.C., 1987. Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. *Estuaries* 10, 28-35.
- Loneragan, N.R., Potter, I.C., 1990. Factors influencing the community structure and distribution of different life-cycle categories of fishes within the shallow waters of a large Australian estuary. *Mar. Biol.* 106, 25-37.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation and recovery potential of estuaries and coastal seas. *Science* 312, 1806-1809.

- Maceina, M.J., Bayne, D.R., 2001. Changes in the black bass community and fishery with oligotrophication in West Point Reservoir, Georgia-Alabama. *N. Am. J. Fish. Manag.* 21, 745-755.
- Minns, C.K., 2009. The potential future impact of climate warming and other human activities on the productive capacity of Canada's lake fisheries: a meta-model. *Aquat. Ecosyst. Health Manag.* 12, 152-167.
- Morison, A.K., Coutin, P.C., Robertson, S.G., 1998. Age determination of black bream, *Acanthopagrus butcheri* (Sparidae), from the Gippsland lakes of south-eastern Australia indicates slow growth and episodic recruitment. *Mar. Freshwater Res.* 49, 491-498.
- Nixon, S.W., Buckley, B.A., 2002. "A strikingly rich zone": nutrient enrichment and secondary production in coastal marine ecosystems. *Estuar. Coast.* 25, 782-796.
- Paerl, H.W., Hall, N.S., Peierls, B.L., Rossignol, K.L., 2014. Evolving paradigms and challenges in estuarine and coastal eutrophication dynamics in a culturally and climatically stressed world. *Estuar. Coast.* 37, 243-258.
- Pennington, M. 1996. Estimating the mean and variance from highly skewed marine data. *Fish. Bull.* 47, 1623-1624.
- Pichavant, K., Person-Le-Ruyet, J., Le Bayon, N., Sévère, A., Le Roux, A., Quéméner, 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., Quéméner, 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.
- Pombo, L., Rebelo, J.E., Elliott, M., 2007. The structure, diversity and somatic production of the fish community in an estuarine coastal lagoon, Ria de Aveiro (Portugal). *Hydrobiologia* 587, 253-268.
- Potter, I.C., French, D.J.W., Jenkins, G.I., Hesp, S.A., Hall, N.G., DeLestang, S., 2008. Comparisons of the growth and gonadal development of otolith-stained, cultured black bream, *Acanthopagrus butcheri*, in an estuary. *Rev. Fish. Sci.* 16, 303-316.
- Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015. The ways in which fish use estuaries: A refinement and expansion of the guild approach. *Fish Fish.* 16, 230-239.
- 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.
- R Core Team, 2016. R: A language and environment for statistical computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Randall, R.G., Minns, C.K., 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. *Can. J. Fish. Aquat. Sci.* 57, 1657-1667.

- Sarre, G.A., Potter, I.C., 1999. Comparisons between the reproductive biology of the black bream *Acanthopagrus butcheri* (Teleosti: 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.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford, Oxford University Press, pp. 249.
- 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.
- 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.
- Tweedley, J.R., Hallett, C.S., Warwick, R.M., Clarke, K.R., Potter, I.C., 2016. The hypoxia that developed in a microtidal estuary following an extreme storm produced dramatic changes in the benthos. *Mar. Freshwat. Res.* 67, 327-341.
- Tweedley, 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. Cstl Shelf Sci.*, 141, 85-96.
- Valentine-Rose, L., Rypel, A.L., Layman, C.A., 2011. Community secondary production as a measure of ecosystem function: A case study with aquatic ecosystem fragmentation. *Bull. Mar. Sci.* 87, 913-937.
- Valesini, F.J., Cottingham, A., Hallett, C.S., Clarke, K.R., 2017. Interdecadal changes in the community, population and individual levels of the fish fauna of an extensively modified estuary. *J. Fish Biol.* 90, 1734-1767.
- Waters, T.F., 1977. Secondary production in inland waters. *Adv. Ecol. Res.* 10, 91-164.
- Western Australian Department of Water, 2017. River Monitoring Stations. Government of Western Australia. <http://kumina.water.wa.gov.au/waterinformation/wir/reports/publish/616011/g02.htm>. Accessed 04.01.17.
- Wakefield, C.B., Potter, I.C., Hall, N.G., Lenanton, R.C.J., Hesp, S.A., 2015. Marked variations in reproductive characteristics of snapper (*Chrysophrys auratus*, Sparidae) and their relationship with temperature over a wide latitudinal range. *ICES J. Mar. Sci.* 72, 2341-2349.
- Whitfield, A.K., 2016. Biomass and production of fish in estuaries: a South African case study. *J. Fish. Biol.* 89, 1971-1930.
- 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.
- Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. *Mar. Pollut. Bull.* 45, 35-45.

LIST OF FIGURES

Figure 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.

Figure 2 Length and age-frequency distributions for *Acanthopagrus butcheri* collected in the Swan River Estuary in each year of 1993/94, 1994/95 and 2007/08 to 2010/11. Grey bars denote data derived from seine catches and white bars from gill net catches. Gill netting was discontinued in 2009/10.

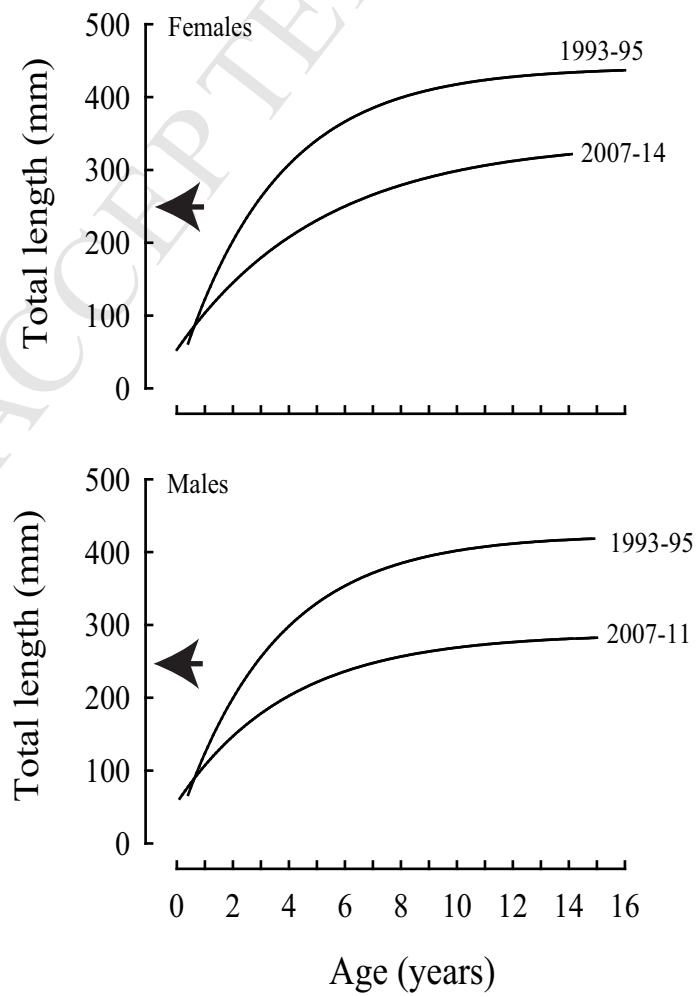
Figure 3 von Bertalanffy growth curves for females and males of *Acanthopagrus butcheri* in the Swan River Estuary in 1993-95 and 2007-11. Figure modified from Fig. 5 in Cottingham et al. (2014). Arrows denote minimum legal length for retention of *Acanthopagrus butcheri*.

Figure 4 Box and whisker plots showing model-derived estimates of (a, d) abundance, (b, e) biomass, (c, f) production and (g, h) production to biomass ratio for *Acanthopagrus butcheri* in (a-c, g) the nearshore waters and (d-f, h) the offshore waters of the upper Swan River Estuary in each year of 1993/94, 1994/95 and 2007/08 to 2010/11. Horizontal line inside each box represents the median value, the bottom and top of each box the 25 and 75 percentiles, and the lower and upper bars the 10 and 90 percentiles, produced when the model was fitted to 1000 bootstrapped data sets. Note offshore, deeper waters were not sampled in 2009/10 and 2010/11.

Figure 5 Box and whisker plots showing predicted annual increases in the mass of one year old *Acanthopagrus butcheri* in the Swan River Estuary during each year of 1993/94, 1994/95 and 2007/08 to 2010/11, using the expected mass at a common starting total length of 115 mm, the approximate length at the commencement of the second year of life. For each scenario the line inside the box shows the median values, the bottom and top of the box show the 25th and 75th percentiles, and the lower and upper bars the

10 and 90 percentiles, produced using year/sex specific mass-length relationships and the 2000 model-derived estimates of the year-specific growth for females and males.

ACCEPTED MANUSCRIPT



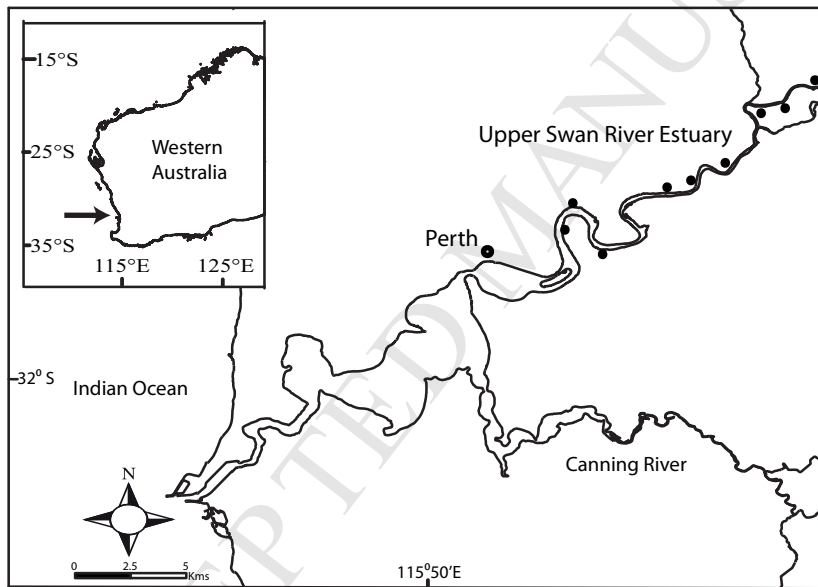


Fig. 1

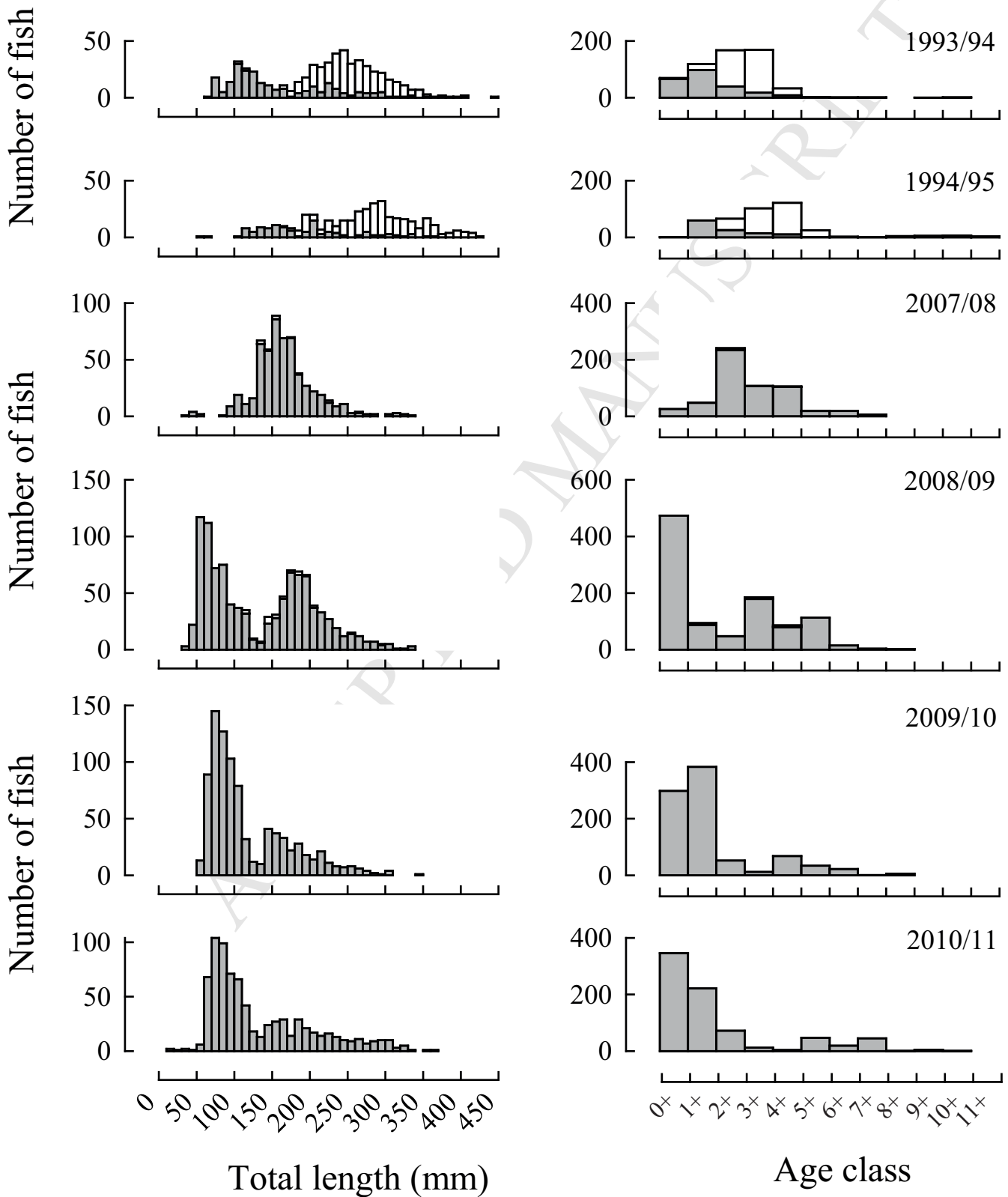


Fig. 2

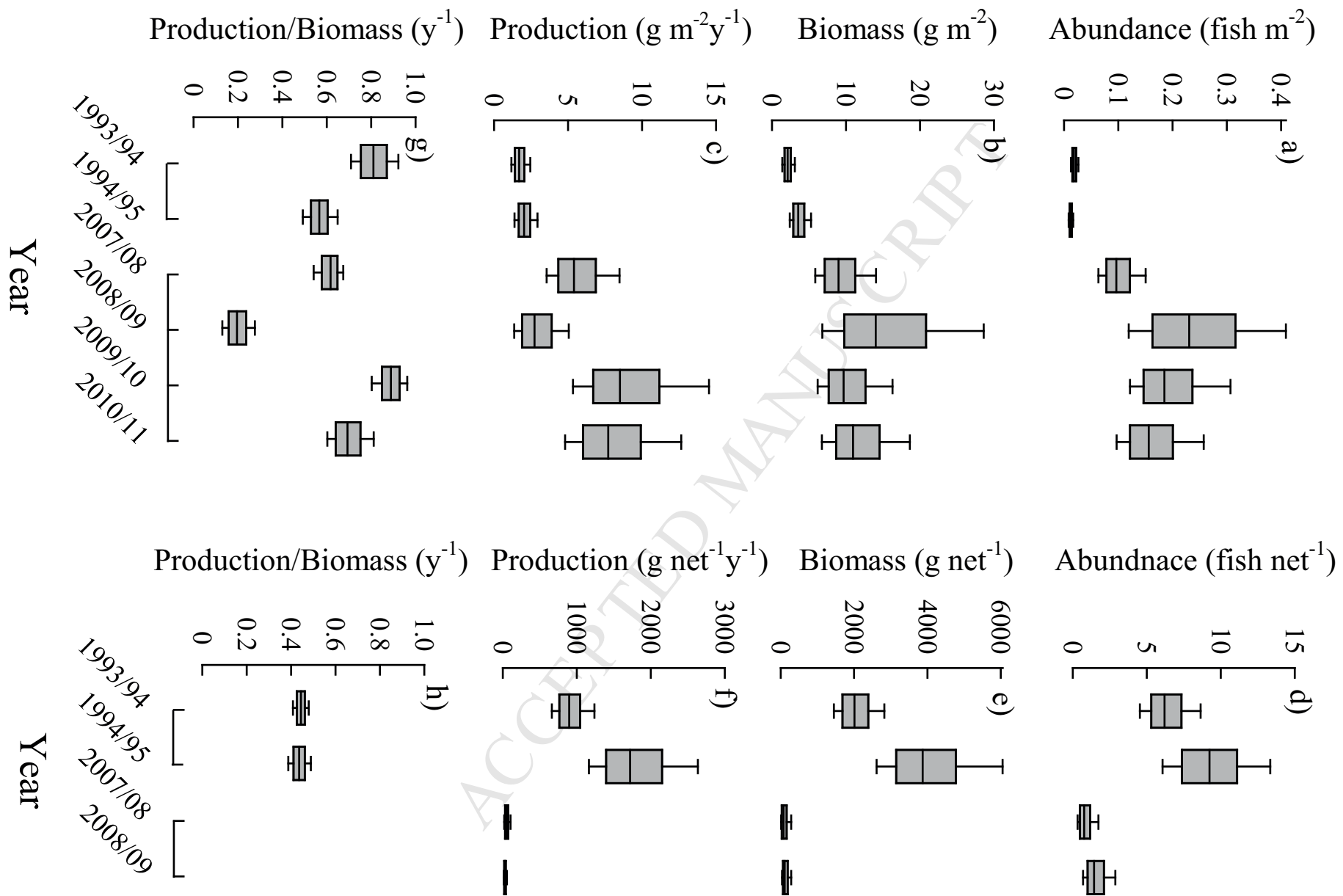


Fig. 4

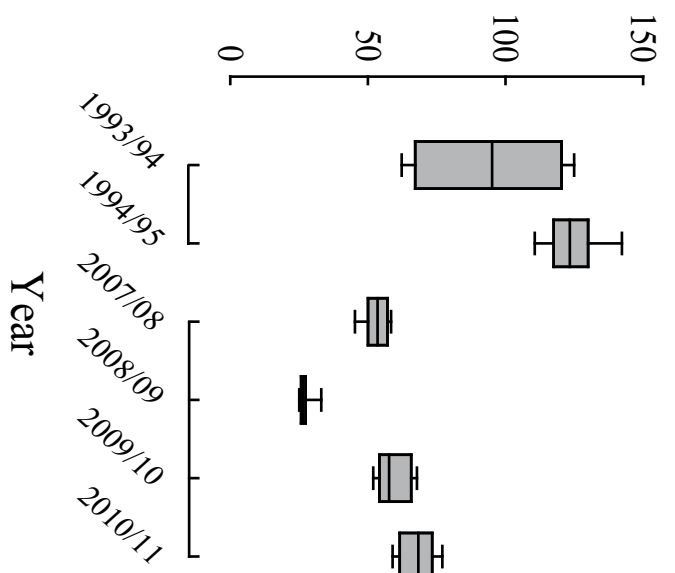


Fig. 5

Highlights

An increase in hypoxia in deep waters of the Swan Estuary between early 1990s and mid-2000s resulted in Black Bream congregating in the shallow waters. Between 1993-95 and 2007-11 growth declined markedly and varied among years within periods. Consequently, biomass and production fell by over 30 times in the deep waters, whereas they increased by three to four times in the shallow waters. Production to biomass ratios were similar among periods except in one particularly cool year.