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Highly variable recruitment in an estuarine fish is determined by salinity stratification and freshwater flow: implications of a changing climate

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ABSTRACT: Estuarine-dependent fish live in a complex and dynamic environment that is primarily influenced by the salinity structure resulting from the mixing of fresh and marine waters. In response to this variable environment, the recruitment of estuarine-dependent fish can also be highly variable. Recruitment variability in black bream *Acanthopagrus butcheri* in Gippsland Lakes, southeastern Australia, was determined both from annual recruitment monitoring and the age structure of the population. Recruitment was found to be episodic, with the population dominated by a few year classes. For the 2 methods of estimating recruitment and associated time periods, we found a consistent linear relationship between water column stratification (difference between surface and bottom salinity) and recruitment. There was also a significant, non-linear (dome-shaped) relationship between freshwater flow and recruitment. This relationship suggested that the highest recruitment occurred at intermediate flows greater than ~3000 Ml d^{-1} in the main tributary rivers. The combination of stratification and freshwater flow in a multiple regression model improved the variability in recruitment explained to 71 and 79%, respectively, for the 2 methods. Analysis of age structure of bream from other Victorian estuaries showed that, as in Gippsland Lakes, recruitment was highly variable and episodic; however, the timing of strong and weak year classes varied between estuaries. This suggests that freshwater flow and salinity structure, and consequent recruitment variability, are unique to each estuary based on characteristics of catchment, channel topography, and entrance opening and closing. Climate change predictions for the Gippsland Lakes region include less rainfall and higher evaporation, potentially leading to higher salinities and lower stratification in Gippsland Lakes. The bream population is therefore likely to be negatively affected, and these effects may be exacerbated by any human activities in the catchment that further reduce freshwater flows or increase marine incursion.

KEY WORDS: Year-class strength · Salinity · Population dynamics · Estuary · Black bream · *Acanthopagrus butcheri* · Gippsland Lakes

INTRODUCTION

Estuarine fish populations can show high recruitment variability as a result of the interaction between the survival of the youngest stages and the complex physical environment they inhabit (Attrill & Power 2002, North & Houde 2003). Recruitment variability can have a strong influence on the population dynamics of fish (Doherty & Fowler 1994, Houde 2008), including long-lived estuarine fish species, where the population can be supported by a few outstanding year classes (Morison et al. 1998). However, recruitment variability may not necessarily determine the trajectory of population abundance where density-dependent mortality is significant (Kimmerer et al. 2001, Houde 2008).

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Freshwater flow is the principal physical variable that determines the characteristics of an estuary (Kimmerer 2002b). A number of studies have demonstrated a positive relationship between freshwater flow and recruitment variability of estuarine-dependent fish (Kimmerer et al. 2001, North & Houde 2003, Staunton-Smith et al. 2004, North et al. 2005, Robins et al. 2005) and invertebrates (Robins et al. 2005). In other cases, however, high freshwater flows can have a detrimental effect on recruitment (Deegan 1990, Rulifson & Manooch 1990, Sarre & Potter 2000, Shoji et al. 2006), with intermediate flows resulting in the highest recruitment success (Rulifson & Manooch 1990, Shoji et al. 2006).

Estuarine systems are characterised by variable salinity characteristics in relation to the amount of freshwater flow (Kurup et al. 1998). Salinity structure has been found to influence the recruitment of estuarine-dependent fish. For example, the low salinity zone where freshwater first meets saltwater, and the associated estuarine turbidity maximum (ETM), has been shown to encompass high zooplankton productivity and higher abundances of larval anadromous fish (Sirois & Dodson 2000, North & Houde 2001, 2003). In some cases, larval abundances seem to be greater in years of higher freshwater flow, possibly owing to enhanced prey productivity, increased retention of larvae and prey in the ETM region or increased spatial overlap of larvae with high prey concentrations and turbidities, resulting in high growth but low predation mortality (North & Houde 2003, Shoji et al. 2005).

The variability and magnitude of freshwater flows to estuaries, and the salinity structure of estuaries, is undergoing change. Flows may be reduced through human activities, such as building dams, and water abstraction or diversion for human consumption, industry, agriculture and aquaculture (Kimmerer 2002b). Salinity structure may also be affected by human activities such as maintaining artificial entrances to estuaries that would otherwise be closed to the sea for varying periods. There are competing needs for human use and the maintenance of ecosystem services (Kimmerer 2002b). Freshwater flows may also be in decline in some areas through reduced rainfall and/or increased evaporation resulting from climate change (Meynecke et al. 2006).

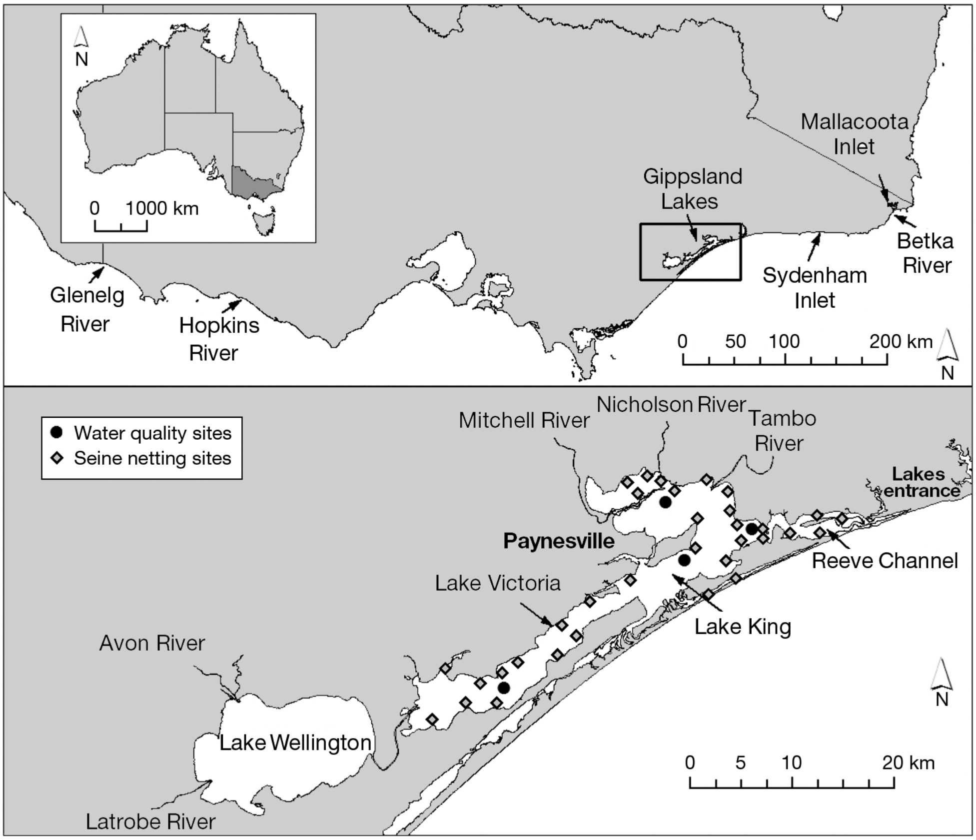

Fig. 1. The Gippsland Lakes and the smaller estuaries (Glenelg River, Hopkins River, Sydenham Inlet, Betka River and Mallacoota Inlet) on the Victorian Coast. Bottom: Gippsland Lakes and major tributary rivers. Positions of Environment Protection Authority of Victoria water quality monitoring stations (●) and beach seine net sampling sites (◇) are also shown

Black bream *Acanthopagrus butcheri* occur throughout southern Australia in estuarine systems and support important commercial and recreational fisheries in certain areas such as the Gippsland Lakes in southeastern Australia (Kailola et al. 1993) (Fig. 1). The commercial black bream fishery has shown a long-term trend in the Gippsland Lakes over the past 100 yr, with a period of moderate catches from 1910 to 1930, low catches from 1930 to 1960, followed by high catches from 1960 to 1990 (Fig. 2). It is possible that this trend is part of a long-term (~50 yr) cycle. Within this long-term trend there have been large fluctuations in catch on a scale of a few years (Fig. 2). Since the mid-1980s, catches have been in decline and reached very low levels in 2000 that continue to the present day (Fig. 2). The recent decline has corresponded with a period of extended rainfall deficit (>10 yr) in the region. Fishing effort has been recorded since 1978 and, in the period since, raw catch and catch per unit effort (CPUE) have shown a similar trend, indicating that variable effort is not the reason for the catch variability (Fig. 2).

Black bream spawn from late winter to early summer in southern Australia, predominantly in salinities >10 (Newton 1996, Haddy & Pankhurst 1998, Walker & Neira 2001, Nicholson et al. 2008). Laboratory studies have shown that egg survival and hatching is greatest in waters with salinities >10 (Haddy & Pankhurst 2000), and larvae in the laboratory have shown high levels of deformity at salinities <15 (Haddy & Pankhurst 2000). Eggs are neutrally buoyant at intermediate salinities and, therefore, tend to accumulate in the region of the salt wedge when developed (Newton 1996, Jenkins et al. 1999). A previous study has shown that black bream in the Gippsland Lakes lived to 29 yr old, and that episodic recruitment resulted in the population being dominated by a few exceptional year classes (Morison et al. 1998).

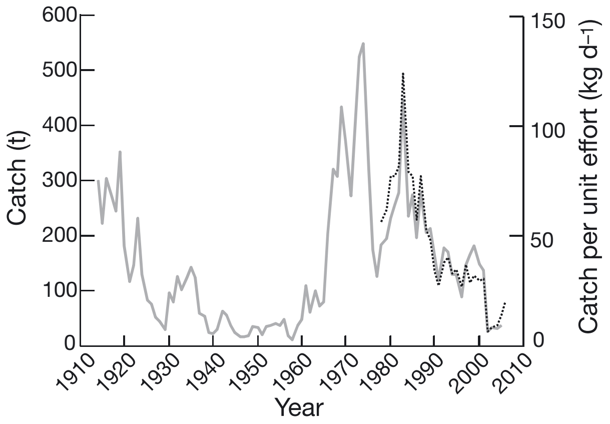

Fig. 2. *Acanthopagrus butcheri*. Historical catch (solid line) and catch per unit effort (dotted line) of black bream from the Gippsland Lakes

In the present study we investigated the hypothesis that recruitment of black bream in Gippsland Lakes is related to freshwater flow and water column stratification, depending on the development of a halocline in the preferred salinity range for bream reproduction. On the basis of knowledge of the early life history of black bream, we postulated that water column stratification and freshwater flow were potentially important variables influencing recruitment variability. We used the age structure of the bream population, as well as annual monitoring of the youngest age classes, to estimate recruitment variability and relate this to water column stratification and freshwater flow into the Lakes. The approach was to not undertake correlations with many possible environmental variables, as this can lead to the identification of spurious correlations with little biological meaning (Walters & Collie 1988). Instead, analyses were based on the known life history of the species and a specific hypothesis relating to the effect of environmental variables based on this information. The implications of the results in terms of future climate change scenarios are discussed.

MATERIALS AND METHODS

Study area. The present study was conducted in the Gippsland Lakes, southeastern Australia (Fig. 1). These lakes are Australia's largest lagoonal estuarine system, covering 600 km^2. The Lakes system has a low (<30 cm) tidal range and is connected to the open ocean by an artificial channel that was cut across the beach at Lakes Entrance in 1889 to stabilise the water level, create a harbour for fishing boats and open up the lakes to shipping (Fig. 1).

Lakes Wellington, King and Victoria are the largest of the lakes in the system. There are 5 major rivers entering the lakes, 2 in the west (the Avon and Latrobe Rivers), and 3 feeding the central basin of Lake King (the Mitchell, Nicholson and Tambo Rivers) (Fig. 1). Their catchments drain 10 % of the freshwater flows in the State of Victoria. The Gippsland Lakes are ~70 km long, forming the largest navigable network of inland waterways in Australia.

Rainfall in the Gippsland Lakes region is not strongly seasonal, but decreased evaporation and the effect of snow melt generally lead to increased river discharges in winter–spring (Webster et al. 2001). Salinity is affected by this seasonal pattern as well as short-term rainfall and/or discharge events (Webster et al. 2001). Lake Wellington is characterised by a well-mixed water column of low salinity, whereas Lakes Victoria and King tend to be stratified with increasing salinity towards Lakes Entrance (Poore 1982) (Fig. 1). Water temperatures in the Lakes reach a maximum of ~22°C in January and a minimum of ~10°C in July (Webster et al. 2001).

Lake Wellington is relatively distinct from the remaining lakes hydrologically (Sakov & Parslow 2004) and ecologically (Poore 1982) and has not been a significant part of the fishery for over 30 yr. Therefore, biological and physico-chemical data from Lake Wellington, and flow data from associated rivers (Latrobe and Avon), were not included in this analysis.

A comparative analysis was also undertaken of smaller estuaries along the Victorian coast: the Glenelg and Hopkins Rivers in the west, and Sydenham Inlet, the Betka River and Mallacoota Inlet in the east (Fig. 1). Unlike the Gippsland Lakes, all of these estuaries are intermittently closed to the sea under conditions of low freshwater flow.

Age analysis. Otoliths from black bream in the Gippsland Lakes and tributary rivers were obtained from commercial haul-seine and mesh-net catches (1993–2002); recreational diary anglers, fishing for research purposes (1997–2004); and annual fishery-independent surveys conducted using a beach seine at over 30 sites from the western end of Lake Wellington to Lakes Entrance (Fig. 1) from 1996 to 2004. The latter surveys aimed to estimate the numbers of pre-recruit black bream in the lakes, but also sampled larger bream. These surveys were usually conducted in February and November of each year and the net (175 m long, 3 m drop, 38 mm mesh in wings and 16 mm mesh in bunt) fished to ~200 m from shore and covered an area of ~4750 m^2. Otoliths of black bream were also obtained from recreational diary anglers fishing for research purposes in the smaller estuaries (1997–2002). The method, validation and precision of ageing black bream otoliths have been previously described by Morison et al. (1998).

Physical data. The Environment Protection Authority of Victoria has been measuring physical and chemical variables at ~0.5 m from the surface and 0.5 m from the bottom at 5 sites in the Gippsland Lakes at 1 to 4 mo intervals since 1986. Salinity data from 4 sites, located in Lake Victoria and north, south and east Lake King, were used in this study (Fig. 1). Surface and bottom salinities were averaged across the sites and sampling times for the months of July to December (the approximate spawning season). An index of water column stratification was then estimated by subtracting the mean surface salinity from the mean bottom salinity to give an annual estimate.

Flow (discharge, ml d^{-1}) data are recorded for each river system entering the Gippsland Lakes and are stored at the Victorian Water Resources Data Warehouse (www.vicwaterdata.net/vicwaterdata/home.aspx). Daily flow data over the period of the present study were extracted and annual mean daily flows were calculated for the July to December spawning period. Mean daily flows of the Mitchell, Nicholson and Tambo Rivers were summed to derive a 'combined' flow estimate.

Data analysis. Recruitment variability estimated from research seine sampling was determined from the number of 0+, 1+ and 2+ age fish in each year's samples (1996–2004), allocating the numbers to the appropriate year class, and then averaging across the age classes for each year class. Because subsampling of the catch was sometimes required, the total number sampled in each year class was calculated by apportioning the numbers in each size class to the year classes using the age–length key for that year. Estimates for the 1995 year class were based on their abundance as 1 and 2 yr olds (sampled in 1996 and 1997), estimates for the 1994 year class were based on their abundance as 2 yr olds only (sampled in 1996), estimates for the 2004 year class were based on their abundance as 0 yr olds (sampled in 2004) and estimates for the 2003 year class were based on their abundance as 0 and 1 yr olds (sampled in 2003 and 2004). As such, estimates for these years may be less reliable than other years where estimates were based on the abundance of the year class as 0, 1 and 2 yr olds.

Recruitment variability was estimated from the age structure of the sampled bream using catch curve regression (the natural log of the number of fish classified to each year class regressed against age) following the methods of Maceina (1997) and Staunton-Smith et al. (2004). We assumed that deviation from the catch curve regression was a reflection of variable recruitment (Staunton-Smith et al. 2004), with large positive and negative studentised residuals representing strong and weak year classes, respectively (Halliday et al. 2008).

The age-frequency data determined from research seine sampling were analysed for recruitment variability because this method sampled small individuals more efficiently than the other methods. Bream were considered to be fully susceptible to the research seine by age 1. Ageing samples from 5 yr (1997–2001) were included in the analysis, and the oldest fish analysed were from the 1987 year class, whereas the youngest were from the 2000 year class. The 1990 cohort was not included owing to a lack of data on salinity in the July–December period.

Statistical analysis. For recruitment estimated from research-seine monitoring, simple and multiple linear regression were used to examine the relationship between recruitment variability and the environmental variables water column stratification and freshwater flow. Residual plots were examined when undertaking regression analyses to check assumptions relating to homogeneity of variance, non-linearity, leverage and outliers (Quinn & Keough 2002).

RESULTS

Age structure

For the commercial seine, age structure for samples collected from 1993 to 1996 was dominated by the 1987 and 1989 year classes. In 1997 and 1998, the 1987 year class declined in importance whereas the 1995 year class was relatively important (Fig. 3). In 2001, smaller individuals dominated and in both 2001 and 2002, the 1995 year class was still important and individuals from the 1989 and 1987 year classes were still present (Fig. 3). For the research seine, age structures for samples collected from 1997 to 2001 were dominated by the 1989 and 1995 year classes whereas, in 2002, young (1 and 2 yr old) individuals dominated (Fig. 4). For angling, age structures for samples collected from 1997 to 2001 were dominated by the 1989 and 1995 year classes. Samples from 2002 and 2003 indicated that the 1998 year class was relatively strong, whereas the sample from 2004 suggested that the 2001 year class was also relatively strong (Fig. 5). Overall, the age structure of black bream collected by 3 sampling methods showed highly variable recruitment, with the 1989 and 1995 year classes and, to a lesser extent, the 1987, 1998 and 2001 year classes, dominating the samples.

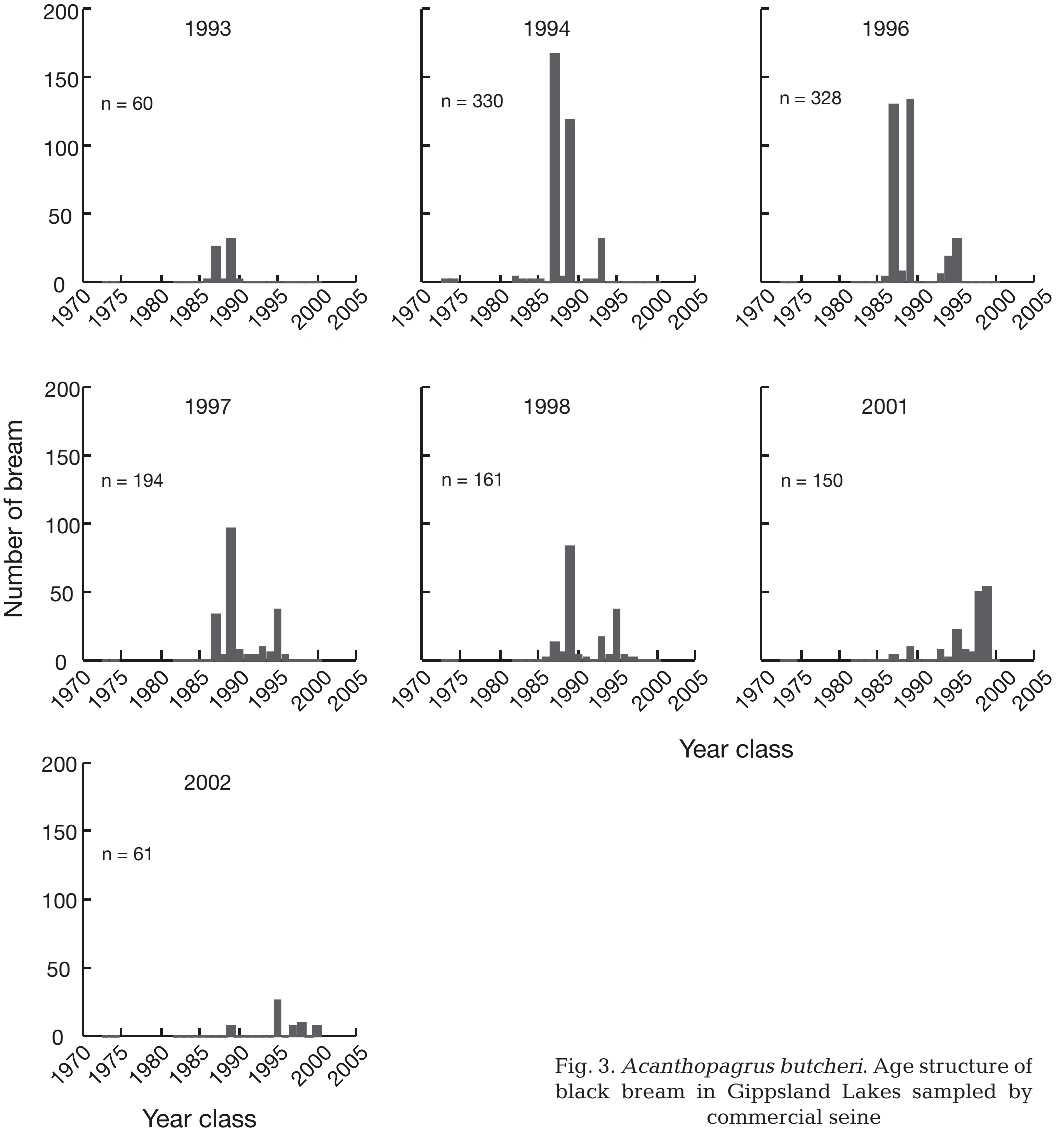

Fig. 3. *Acanthopagrus butcheri*. Age structure of black bream in Gippsland Lakes sampled by commercial seine

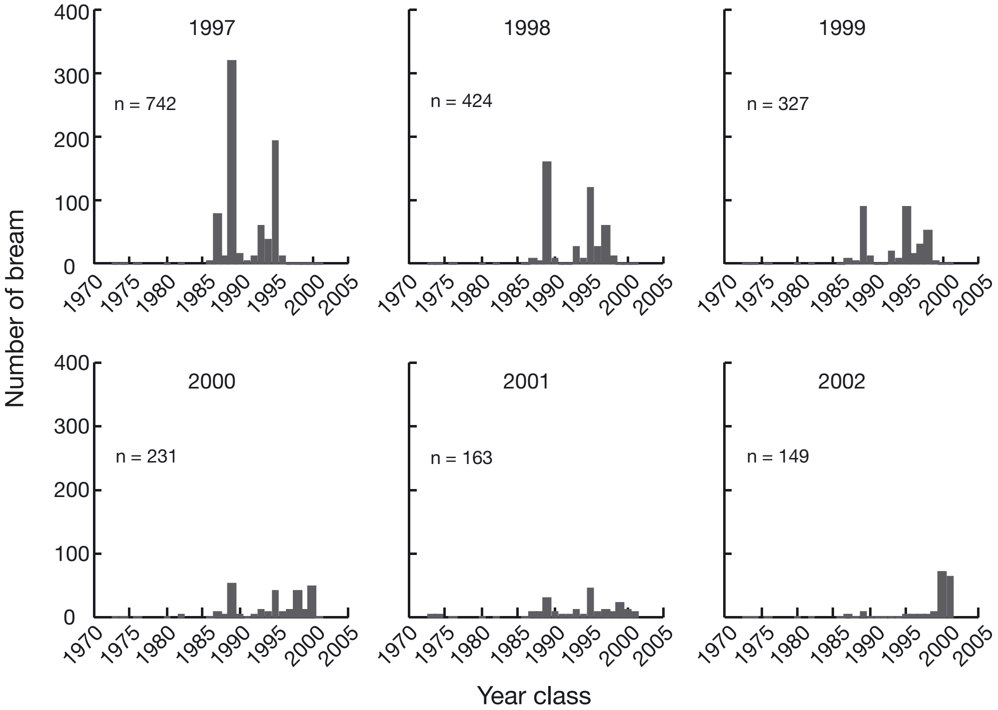

Fig. 4. *Acanthopagrus butcheri*. Age structure of black bream in Gippsland Lakes sampled by research seine

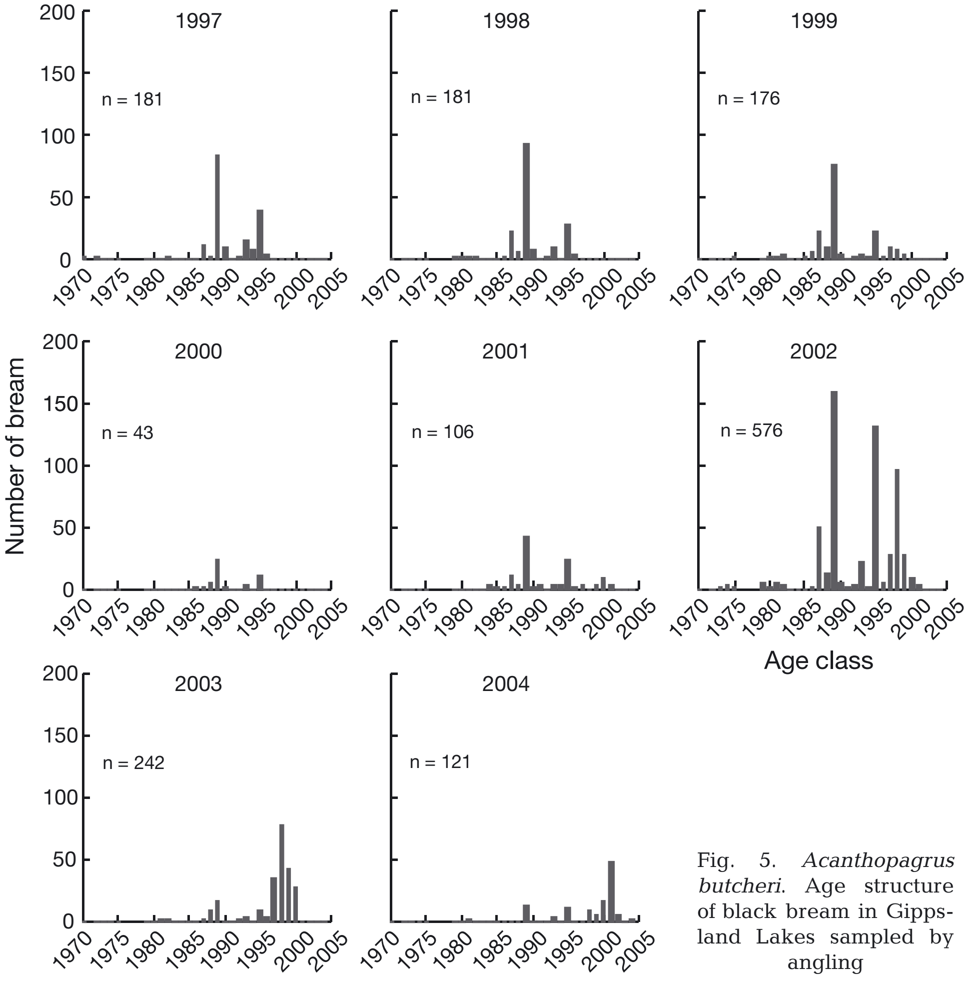

Fig. 5. *Acanthopagrus butcheri*. Age structure of black bream in Gippsland Lakes sampled by angling

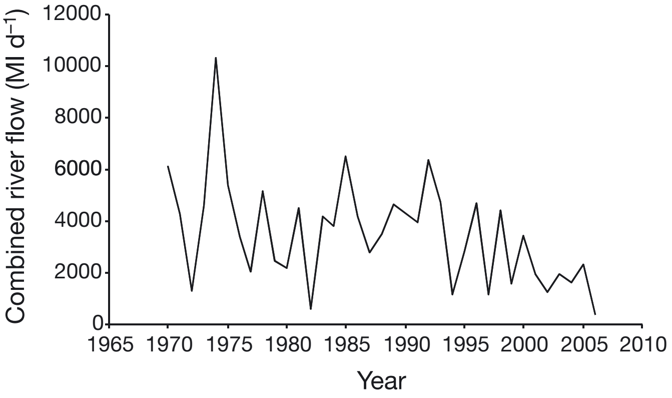

Fig. 6. River flow (mean daily) for the Mitchell, Tambo and Nicholson Rivers combined, for July to December

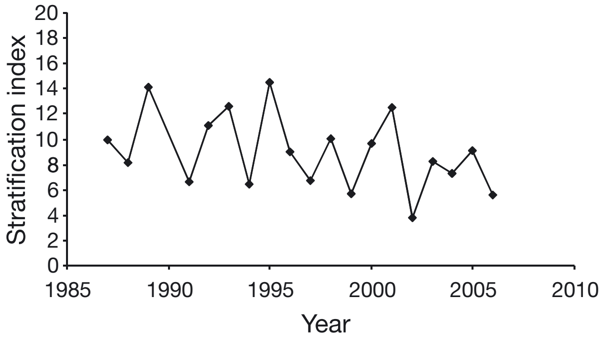

Fig. 7. Annual estimates of the stratification index (mean bottom salinity minus mean surface salinity) for July to December

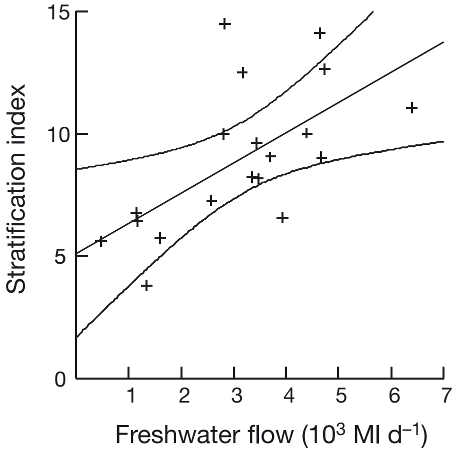

Fig. 8. Relationship between annual river flow (mean daily) for the Mitchell, Tambo and Nicholson Rivers combined and the annual estimate of the stratification index (mean bottom salinity minus mean surface salinity) for July to December. Linear regression line and 95% confidence intervals are also shown

Stratification and flow

Annual mean flows from July to December of rivers entering the eastern Gippsland Lakes have shown considerable variability since 1970, ranging from 10 000 Ml d^{-1} in 1974 to <1000 Ml d^{-1} in 1982 and 2006 (Fig. 6). Flows in the middle of the time series from 1983 to 1993 were less variable than the period before or after (Fig. 6). Flows showed a decreasing trend from about the mid-1990s, corresponding to an extended drought over the period (Fig. 6).

The stratification index (the difference between annual mean surface and bottom salinities) was variable from year to year and showed peaks in 1989, 1993, 1995, 1998 and 2001 (Fig. 7). There was also a general downward trend in the index (Fig. 7), consistent with a narrowing of the difference between surface and bottom salinities over time.

Time series of freshwater flow and stratification showed no significant autocorrelation. Over the whole time series, the linear relationship between freshwater flow and stratification (Stratification = 0.00124 × Flow + 5.11204) was significant (R = 0.63, $F_{1,17}$ = 11.25, p = 0.004). Stratification was generally lower for flows below 2000 ml d^{-1} but was quite variable at higher flows, with the highest levels of stratification occurring at flow levels ranging from 2500 to 5000 Ml d^{-1}, although low stratification could also occur in this flow range (Fig. 8).

Recruitment variability

Peaks in recruitment estimated from the research-seine sampling occurred in 1995, 1998, 2001 and 2003 (Fig. 9A), matching quite well the pattern of peaks in the stratification data (Fig. 7). Peaks in recruitment estimated from the age structure (studentised residuals from the catch curve regression for samples of bream from each of the years 1997–2001) occurred in 1989, 1995 and, to a lesser extent 1987, 1993 and 1998 (Fig. 9B). The pattern of recruitment estimated from residuals of the catch curve matched the stratification data well between 1987 and 1996 but was less well matched thereafter (Fig. 7). This may be partly due to the lower number of residuals used in the estimate for the most recent years.

Relationship between recruitment variability and physical variables

Recruitment estimated from research-seine monitoring

The time series of recruitment estimated from research-seine monitoring showed no significant auto-

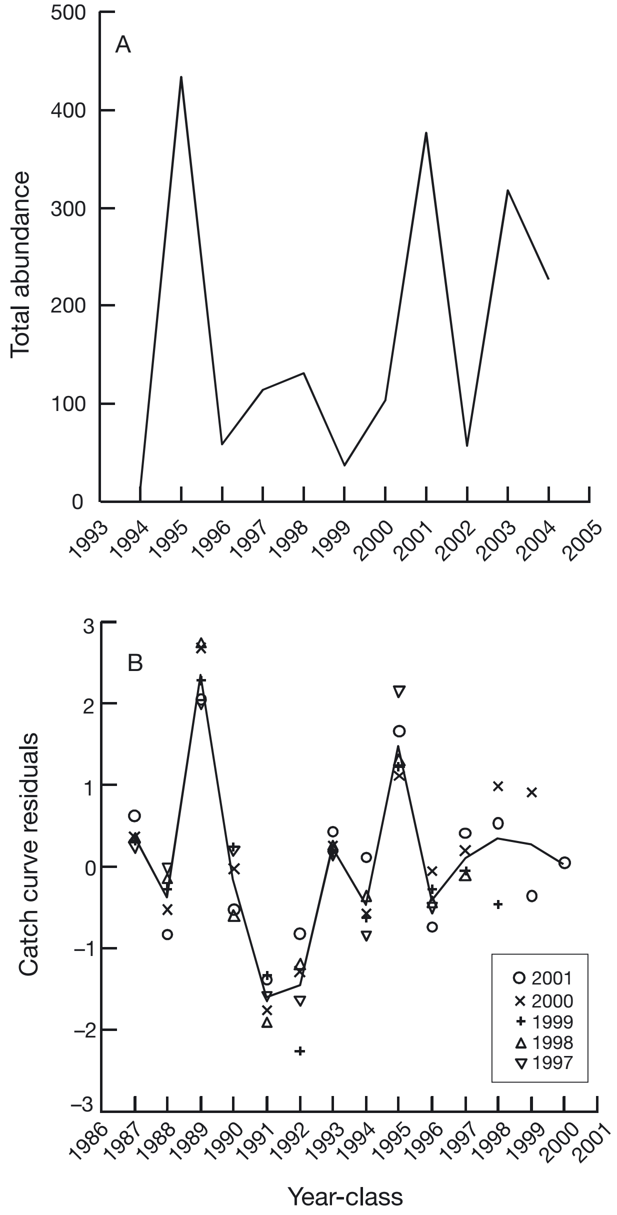

Fig. 9. *Acanthopagrus butcheri*. Recruitment of black bream estimated by (A) total abundance of 0+, 1+ and 2+ age black bream caught in annual research seine surveys, or (B) standardised residuals (data points) and average of the residuals (solid line) from catch-curve regression of the age structure of black bream sampled by research seine over 5 yr

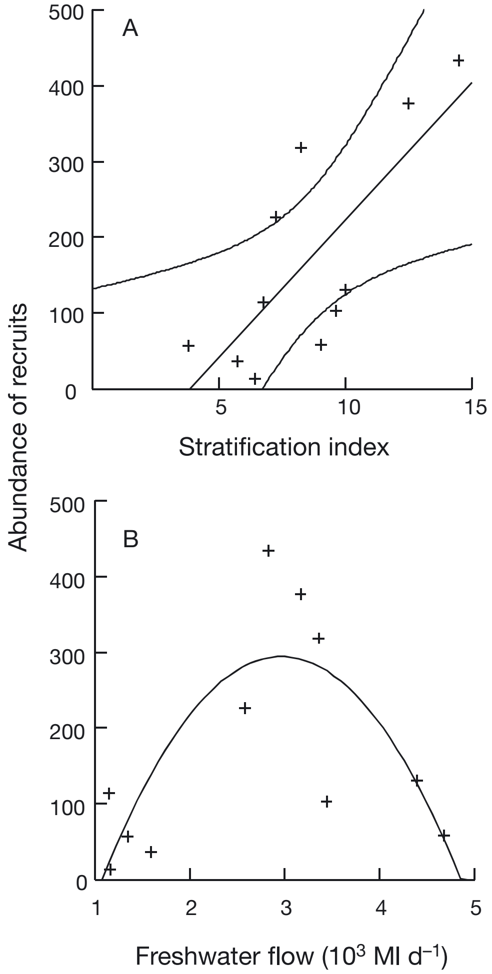

Fig. 10. *Acanthopagrus butcheri*. Relationship between recruitment of black bream estimated by total abundance of 0+, 1+ and 2+ age black bream caught in annual research seine surveys and (A) the stratification index (linear regression line and 95% confidence intervals are also shown) or (B) river flow (mean daily) for the Mitchell, Tambo and Nicholson Rivers combined (polynomial regression line is also shown), for July to December

correlation. The regression between stratification and recruitment (Recruitment = 36.2606 × Stratification – 139.1789) was significant (R = 0.76, $F_{1,9}$ = 12.376, p = 0.007), with 58% of the recruitment time series explained by stratification (Fig. 10A). The regression between freshwater flow and recruitment, however, was not significant (R = 0.28, $F_{1,9}$ = 0.755, p = 0.470), but there was evidence of curvilinearity in the residuals. A second-order polynomial regression (Recruitment = 0.4876 × Flow – 0.00008 × Flow^2 – 428.3755) was significant (R = 0.79, $F_{1,9}$ = 6.561, p = 0.02), with 62% of the recruitment explained by flow (Fig. 10B). This relationship suggested that there was a peak in recruitment when combined freshwater flow for the June–December period averaged ~3000 Ml d^{-1} (Fig. 10B). A multiple regression including both stratification and flow terms (Recruitment = 28.3302 × Stratification + 0.2942 × Flow – 0.00005 × Flow^2 – 389.9336) was highly significant (R = 0.89, $F_{3,7}$ = 9.032, p = 0.008), with 79% of the recruitment variability explained.

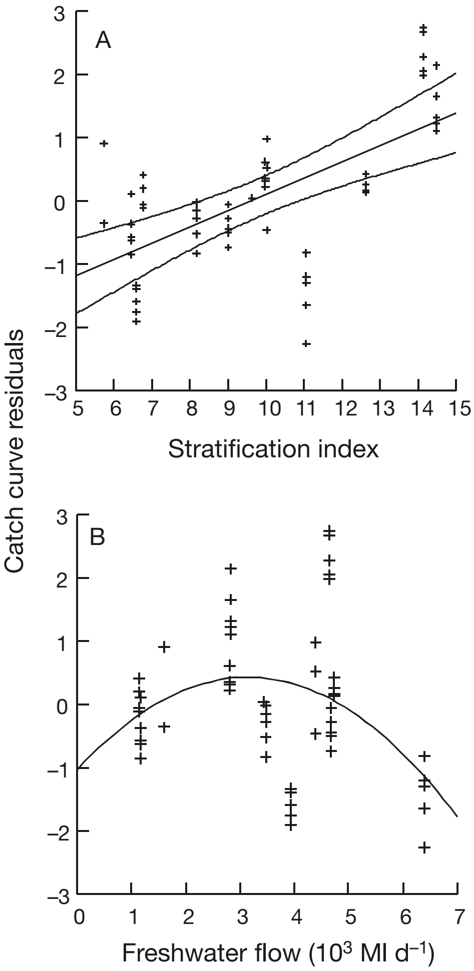

Fig. 11. *Acanthopagrus butcheri*. Relationship between recruitment of black bream estimated by standardised residuals and average of the residuals from catch-curve regression of the age structure of black bream and (A) the stratification index (linear regression line and 95% confidence intervals are also shown) and (B) river flow (average daily) for the Mitchell, Tambo and Nicholson Rivers combined (polynomial regression line is also shown), for July to December

Recruitment estimated from age structure

The time series of residuals from catch curve analysis showed no significant autocorrelation. The regression between the catch curve residuals and stratification (Recruitment = 0.2574 × Stratification − 2.4763) was significant ($R = 0.64$, $F_{1,53} = 37.149$, $p < 0.001$), with 41% of the variance explained (Fig. 11A). The regression between the catch curve residuals and freshwater flow (Recruitment = -10^{-4} × Flow + 0.4539) was not significant ($R = 0.15$, $F_{1,53} = 1.187$, $p = 0.281$). However, a second-order polynomial regression (Recruitment = 0.00093 × Flow + 10^{-7} × Flow^2 − 1.03420) was significant ($R = 0.37$, $F_{2,52} = 4.249$, $p = 0.020$), with 14% of the recruitment explained by flow (Fig. 11B). A multiple regression including both stratification and flow terms (Recruitment = 0.3594 × Stratification + 10^{-5} × Flow − 10^{-7} × Flow^2 − 2.5431) was highly significant ($R = 0.84$, $F_{3,51} = 42.34$, $p < 0.001$) with 71% of the recruitment variability explained.

Age structure from other estuaries

Like for the Gippsland Lakes, the age structure of bream sampled from smaller estuaries showed evidence of episodic recruitment (Fig. 12). Age structure in these smaller inlets was quite different to that observed in Gippsland Lakes, and compared with each other (Fig. 12). In the Glenelg River there was a strong cohort of bream that recruited around 1983 (Fig. 12A), whereas in Sydenham Inlet (Fig. 12C) and, to a lesser extent, the Betka River (Fig. 12D) there was strong recruitment in 1988. In Mallacoota Inlet there was strong recruitment in 1993 (Fig. 12E). In Sydenham Inlet there were a number of older fish, up to 39 yr of age (Fig. 12C).

DISCUSSION

We found that water column stratification and freshwater flow are key environmental variables that influence the recruitment of black bream in the Gippsland Lakes. This result supports previous studies that have emphasised the importance of water column stratification in the early life history of black bream. Nicholson et al. (2008) found that bream eggs and yolk-sac larvae were most common in the Glenelg and Hopkins estuaries when the water column was strongly stratified in the spring, confirming the results of a previous study in the Hopkins estuary (Newton 1996). Eggs were mostly found in salinities >10 and often within the halocline around the 20 isopleth (Nicholson et al. 2008). The intermediate buoyancy of bream eggs means that they will accumulate near the halocline in a stratified water column (Jenkins et al. 1999). Recent ichthyoplankton sampling in the Mitchell River upstream from the entrance to Gippsland Lakes in drought conditions has shown that bream eggs and larvae were concentrated around the halocline in a strongly stratified water column (J. Williams unpubl. data).

The intensity of salinity stratification has not previously been identified as a key driver of recruitment for other estuarine species and systems, although other characteristics of salinity structure have been found to be important. For example, eggs and larvae of anadromous fish species have been found to be associated with the ETM that can occur in the low-salinity transition zone where freshwater first meets saltwater in Chesapeake Bay (North & Houde 2003) and the St. Lawrence estuary (Sirois & Dodson 2000). In San Francisco Bay, the position of the low-salinity transition zone with a bottom salinity of 2 (which is associated with an ETM), has been linked to increases or decreases in the abundance or survival of a variety of organisms (Jassby et al. 1995, Kimmerer 2002a), including the survival of egg to young-of-the-year striped bass (Kimmerer et al. 2001).

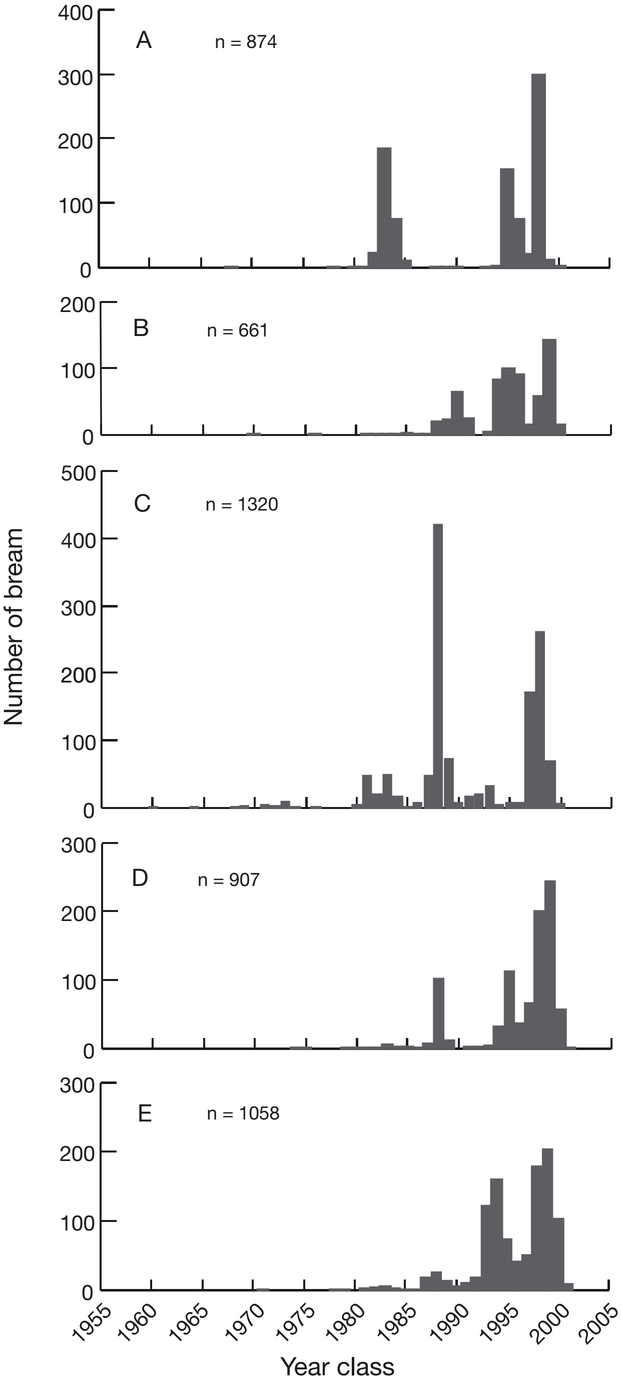

Fig. 12. *Acanthopagrus butcheri*. Age structure of black bream sampled by angling from other Victorian estuaries. (A) Glenelg River, (B) Hopkins River, (C) Sydenham Inlet, (D) Betka River and (E) Mallacoota Inlet

There are several possible reasons for higher bream recruitment when the Gippsland Lakes are more stratified. Stratification may be a cue for bream spawning or may support higher survival of eggs and larvae. Stratification within the Lakes would mean a much larger potentially suitable spawning area than under conditions of low flow when the salt wedge retreats up the rivers and salinities in the Lakes approach marine values, or under flood conditions when most of the Lakes would be freshwater and unsuitable for egg or larval survival. Sarre & Potter (2000) found that a normally closed estuary had a missing year class of bream in a year of cyclonic rainfall and breaching of the mouth that would have resulted in flushing of eggs and larvae from the system. In another example of the effect of salinity fluctuation on recruitment, bream introduced to a land-locked lagoon only showed recruitment in years of salinity >10 (Smith et al. 2009). Spawning within the Lakes rather than up the rivers would also put settling juveniles in close proximity of seagrass habitat that may be beneficial for survival (Ramm 1986). Stratified conditions may lead to increased primary production (Lucas et al. 1998, Kimmerer 2002b), in turn leading to enhanced survival of bream larvae if secondary zooplankton production is also stimulated. Higher concentrations of zooplankton prey for larval fish have been found at the salt front in other systems (Sirois & Dodson 2000, North & Houde 2001, 2003, Shoji et al. 2005). Recent sampling in the Mitchell River has shown high concentrations of copepods (*Gladioferens pectinatus*, the primary prey of black bream larvae) associated with the halocline, and these were also the sites of highest concentrations of larval black bream (J. Williams unpubl. data).

There was a significant curvilinear (domed) relationship between freshwater flow and bream recruitment variability. Freshwater water flow has been shown to positively and linearly influence the recruitment of a number of fish species in estuaries. For example, abundance and survival of early life stages (<1 yr old) of striped bass (Kimmerer et al. 2001, North et al. 2005) are positively related to freshwater flow. For barramundi, strong year classes determined from age structure (Staunton-Smith et al. 2004), and also lagged catch data (Robins et al. 2005), are positively influenced by freshwater flow. Recruitment variability indicated by age structure for king threadfin in a dry-tropical estuary was also shown to be positively related to freshwater flow (Halliday et al. 2008). Not all studies, however, show positive linear effects of flow on estuarine fish (Deegan 1990, Rulifson & Manooch 1990, Sarre & Potter 2000, Shoji et al. 2006). Flow is thought to have a positive influence on Japanese sea perch recruitment, except in years of very high flow (Shoji et al. 2006), suggesting a domed relationship. Intermediate flows have also been shown to be most beneficial for recruitment of striped bass influenced by varying reservoir discharge (Rulifson & Manooch 1990).

Two previous studies have examined the relationship between bream recruitment and freshwater flow into the Gippsland Lakes. Hobday & Moran (1983) related freshwater flow to recruitment variability in the 1970s based on age structure determined from scales and suggested a negative relationship between spring flow and recruitment. Since this study, however, ageing based on scales has been shown to be unreliable (Morison et al. 1998), and the analytical method used was non-quantitative; therefore, the result must be treated with considerable caution. Walker et al. (1998) estimated recruitment variability from the age structure of bream collected in 1997, and, like the present study, found no significant linear relationship between freshwater flow and recruitment. Although some weak correlations were found with other environmental variables (Walker et al. 1998), the large number of tests conducted makes the likelihood of spurious correlations high (Walters & Collie 1988).

The finding of a domed shape relationship between flow and bream recruitment is perhaps not surprising, given that young stages are found in stratified conditions and in intermediate salinities. Very low flows would be likely to result in reduced stratification and an increase in bottom salinities above the preferred range, as has been seen throughout the Lakes in recent drought years. Conversely, very high flows would also reduce stratification and salinities would be below the preferred range for eggs and larvae. Thus, intermediate rather than extreme flows are most likely to result in strong stratification and the preferred salinity range for spawning. The combination of stratification and freshwater flow in multiple regression analysis adds considerably to the variability in recruitment that can be explained. Freshwater flow in the model probably adds information that relates to the nature of the stratification, given that the stratification parameter we used only compares surface and bottom salinities, but does not include information such as the depth of the halocline or the gradient of salinity isopleths through depth. The addition of the flow variable may be providing this extra information; for example, higher flows may result in a deeper halocline for a given level of difference between surface and bottom salinity.

There is always the chance that spurious correlations can occur when relating environmental variables to recruitment variability, particularly when a large number of variables are tested indiscriminately (Walters & Collie 1988). In the present study, we selected 2 variables for analysis based on the known life history characteristics of the species. We used 2 different methods of estimating recruitment variability associated with offset time periods, with similar conclusions drawn for both. Results in relation to environmental variables tended to be more consistent for the seine net survey data, which is understandable given that this is a more direct measure of recruitment than that based on age structure. The advantage of using catch curve residuals based on age structure, however, is that a significant time period of recruitment variability can be generated based on only 1 or a few years of sampling. Although the methods of determining recruitment variability relied on assumptions such as relatively constant mortality across age classes (Staunton-Smith et al. 2004), the very strong episodic variability in recruitment of bream meant that the patterns were likely to be clear even if the assumptions were not entirely met.

The age structure of bream in other estuaries, like the Gippsland Lakes, showed highly variable recruitment. The pattern of strong and weak year classes, however, varied amongst estuaries, indicating that environmental influences on recruitment are unique to each estuary. There were, however, some regional similarities. For example, the 1988 year class was strong in both Syndenham Inlet and the Betka River, in far eastern Victoria. Unlike the Gippsland Lakes, which has a permanent artificial opening, these smaller estuaries maybe closed from the sea under low freshwater flows. We suggest that differences in recruitment among estuaries are likely to be driven by different levels of stratification. The stratification characteristics of each estuary will be unique owing to differences in catchment-based freshwater flow, topography of the estuary and entrance characteristics (timing of opening or closing, etc.), although nearby estuaries may show similar patterns owing to similarity in regional factors such as rainfall patterns. There could also be some mixing of individuals from adjacent estuaries that would tend to homogenise the recruitment patterns at this scale (Burridge et al. 2004).

The recent drought in Victoria has provided a snapshot of the likely impact of climate change on bream recruitment in the Gippsland Lakes. Climate change predictions are for a reduction in flows to Gippsland Lakes of up to 50 % by 2070 relative to the 1980–1999 mean (CSIRO & Australian Bureau of Meteorology 2007). This is a similar reduction to that which has occurred in recent years, owing to an extended drought (Fig. 6). The result of the recent drought is that the Lakes have become more saline and less stratified, and mean surface salinities are regularly higher than the preferred salinity range for bream eggs and larvae. The result of this is that suitable conditions of salinity and stratification are increasingly only found in the tributary rivers. Recent sampling in the Mitchell, Tambo and Nicholson Rivers under dry climatic conditions has shown that significant black bream spawning occurred well upstream from the Lakes where stratification conditions were suitable (J. Williams unpubl. data). Acoustic tagging has also shown that black bream spend the majority of their time in the tributary rivers of the Gippsland Lakes rather than the Lakes themselves under dry conditions (Hindell et al. 2008). Estuarine fish in other systems have been shown to move significantly up- or down-estuary based on fluctuating salinity conditions (Barletta et al. 2005, 2008).

The probable result of retraction of spawning upstream is a reduced area for potential spawning and larval settlement, which has likely contributed to reduced bream recruitment that appears to have been reflected in catches and CPUE in recent years. There is also likely to be a catchability effect because commercial fishing for bream is only allowed in the Lakes, not the tributary rivers. Notwithstanding possible catchability effects, the reduced bream recruitment appears to have been not only reflected in commercial catch rates, but also in catch rates by anglers in the tributary rivers over recent years (S. Conron unpubl. data).

The largest decrease in rainfall in the Gippsland Lakes region under climate change is predicted to occur in spring, coinciding with the bream spawning season in the Lakes. The effect of this reduction in spring rainfall on recruitment depends on whether the spawning season is fixed, based on factors such as increasing day length or water temperature, or whether, as has been suggested for bream populations elsewhere (Smith et al. 2009), the spawning period can shift depending on the timing of suitable salinity conditions. Proposals to construct additional dams on feeder rivers for human water supply or create additional entrances to the lakes to increase marine flushing and reduce problems such as algal blooms would exacerbate the impact of climate change on bream populations. Our results suggest that water managers should aim to maintain intermediate daily flows into the eastern Gippsland Lakes of at least 3000 Ml over the July to December period to sustain a healthy black bream population and fishery.

CONCLUSIONS

Recruitment of black bream in the Gippsland Lakes and other Victorian estuaries was highly variable and episodic. Most of the recruitment variability in the Gippsland Lakes could be explained by water column stratification and freshwater flow. Stratification is known to be a key variable in the early life history of bream, as eggs and larvae are known to occur in the halocline region of stratified water columns at intermediate salinities. Decreased freshwater flows predicted for the Gippsland Lakes region under climate change are likely to lead to increased salinities and decreased stratification in the Lakes, limiting the spawning habitat to tributary rivers and potentially reducing the bream population levels in the Lakes.

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