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Does the quantity and timing of fresh water flowing into a dry tropical estuary affect year-class strength of barramundi (*Lates calcarifer*)?

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Abstract. The influence of fresh water flowing into estuaries on biological processes, such as recruitment of juvenile fish, is poorly understood, but important if freshwater resources are to be managed sustainably. Typically, lagged correlations between freshwater flows and fisheries production (i.e. catch) are used to support speculation that flows affect the survival of fish (and thus year-class strength) during their first year of life. The present study compares the relative strength of year classes in an estuarine fish population with two indices of fresh water flowing into the estuary, river flow and coastal rainfall. Year-class strength was estimated from a subset of the age structure of commercially caught adult barramundi (*Lates calcarifer*), which were sampled at seafood processors for three consecutive years. Strong and coherent fluctuations in year-class strength were observed. Positive correlations were found between the abundance of year classes (accounting for age) and quantity of fresh water flowing into the estuary during spring and summer, when barramundi spawn and young-of-the-year recruit to nursery habitats. Regression analysis was used to explore the relationships between year-class strength and environmental variables. A possible, but unproven, causal mechanism for the relationship is that the quantity of fresh water flowing into the estuary during spring and summer influences the survival of early life-history stages of barramundi (i.e. juvenile recruitment) by altering accessibility, productivity and or carrying capacity of nursery habitats.

Extra keywords: environmental flows, fish recruitment, otoliths, regression analysis, year-class strength.

Introduction

The use of freshwater resources (e.g. for cities, industry and agriculture) has altered the magnitude, duration and timing of fresh water flowing into estuaries and has impacted estuarine species (Drinkwater and Frank 1994; Gillanders and Kingsford 2002). Sustainable management of fresh water requires an understanding of the role (or importance) of freshwater flows in downstream biological processes, and how changing natural river flows impacts estuarine populations. Several estuarine species are exploited by commercial, recreational or subsistence fisheries, and the management of these fisheries would also benefit from an understanding of factors other than fishing effort (i.e. environmental factors) that influence the population size (Shepherd *et al*. 1984; Hilborn and Walters 1992).

The link between freshwater flows and estuarine organisms has often been investigated by comparing catch data from commercial fisheries with patterns in naturally variable, or highly altered, freshwater flows (e.g. Sutcliffe *et al*. 1977; Lloret *et al*. 2001). Significant covariation between flow and catch has been reported for numerous marine and estuarine species, often with time lags equalling the approximate age at which a species enters the fishery (e.g. Lloret *et al*. 2001; Quiñones and Montes 2001). This pattern has been used to generate or support hypotheses that freshwater flows influence the spawning, survival and growth of fish during their first year of life (Drinkwater and Frank 1994). Although some studies have further investigated the variation in abundance and distribution of early life-history stages (e.g. North and Houde 2003), few have been able to confirm the speculated causal mechanisms.

If fresh water flowing into estuaries affects commercial catches by influencing the survival of young fish, then year-class strength (YCS) should vary with freshwater flow and persist through time in order to affect the subsequent abundance of adult fish. Studies of YCS frequently quantify the abundance of specific young age classes on an annual basis (e.g. Helle *et al*. 2000; DiCenzo and Duval 2002; Sutela *et al*. 2002). However, strong and weak year classes can persist through time and are often detected in

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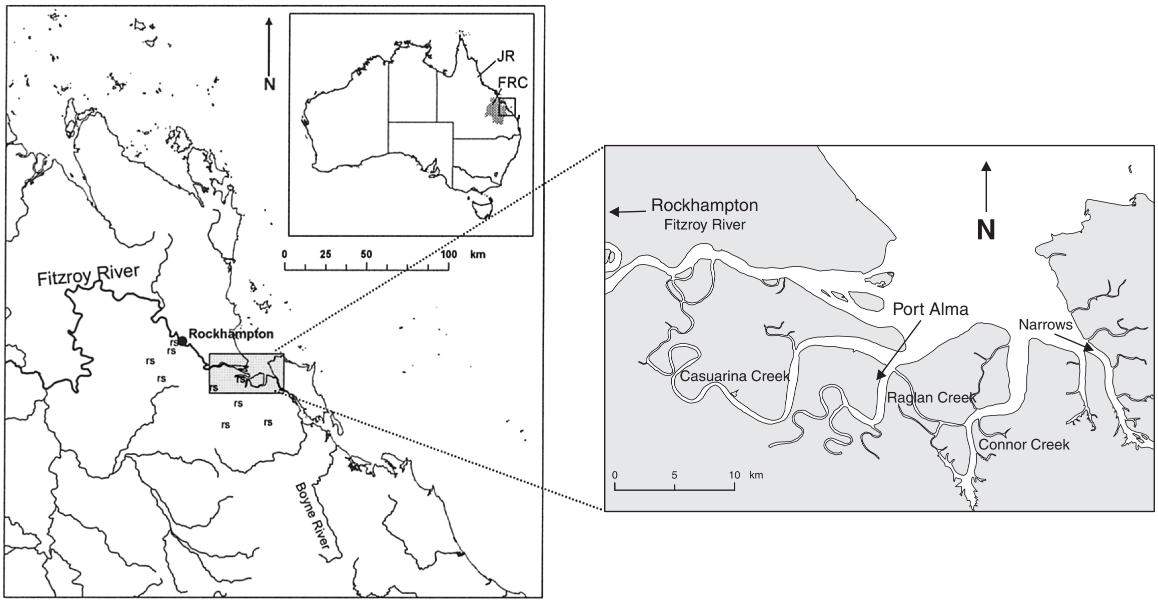

Fig. 1. Location of the Fitzroy River catchment (FRC) and estuary (downstream from Rockhampton) in central Queensland, Australia. Boyne River and Johnstone River (JR) were rivers from which known-age barramundi were collected. rs, Coastal rainfall station.

the age structure of adult populations of freshwater and marine species (e.g. Mills and Mann 1985; Maceina 1997; Morison *et al*. 1998; McGlennon *et al*. 2000; DiCenzo and Duval 2002). Therefore, examining the age structure of an adult population of fish provides an opportunity to examine the relative strength of several consecutive year classes, especially for long-lived species. Such an approach can be completed with relatively few years of sampling compared with surveys of early life-history stages (e.g. 0+ or 1+ age classes), which yield one estimate of year-class strength per year and therefore require many years of sampling.

The aim of the present study was to determine whether there was evidence of variation in YCS in the adult population of a long-lived estuarine fish (barramundi, *Lates calcarifer*) for which large-scale variability in YCS has not yet been demonstrated and, if so, whether the variation could be related to fresh water flowing into the estuary. We examined the age structure of the adult population because of the time efficiency of this approach and because the scale of the estuarine commercial fishery is sufficient to sample the adult barramundi population adequately, thus negating the need to kill large numbers of fish during fishery-independent surveys. The specific objectives of the study were to: (*i*) estimate the age structure of the barramundi population in a dry tropical Australian estuary; (*ii*) estimate YCS; (*iii*) investigate whether variation in YCS was related to patterns in the freshwater flowing into the estuary; and (*iv*) propose possible causal mechanisms for the observed relationships.

Materials and methods

Study area

The Fitzroy River is situated near the Tropic of Capricorn in central Queensland, Australia (Fig. 1). The river has a large catchment of ~142 500 km^2 and a seasonal flow regime of the 'extreme late summer' type as defined by Haines *et al*. (1988) (i.e. dominated by high summer flows and low or zero winter flows). The river has mean and median annual discharges of $\sim 5.2 \times 10^6$ ML (164.8 $m^3 s^{-1}$) and 2.9×10^6 ML (91.9 $m^3 s^{-1}$) respectively.

A tidal barrage was built on the river in the city of Rockhampton in 1970. The barrage defines the upper limit of the estuary, ~50 km from the estuary mouth, by preventing the penetration of tidal/saline waters further upstream. The estuary was reduced in size by the construction of the barrage, from ~140 000 ha to ~70 000 ha (Long and McKinnon 2002). Runoff from rainfall throughout the catchment flows into the mangrove-lined estuary either through the barrage (i.e. via the main river), or via a large number of small- to medium-sized creeks (streams) that enter the river downstream from the barrage.

Study species

Barramundi (*Lates calcarifer*) has an important ecological role in estuaries throughout northern Australia as a large predatory fish (Dunstan 1959) and is socially and economically important to commercial, recreational and indigenous fishers. Numerous aspects of the species' life cycle suggest that fresh water flowing into estuaries may influence survival of young fish and the subsequent size of the adult population several years later (Williams 2002). Therefore, potential negative impacts on barramundi populations, such as through changes to the quantity and timing of fresh water flowing into estuaries, are of concern to natural resource managers.

Barramundi migrate between fresh and saltwater habitats, spawning in the latter (i.e. catadromous; Dunstan 1959; Griffin 1987), and individual fish change sex from male to female (i.e. protandrous; Moore 1979; Davis 1982). However, the life cycle varies substantially throughout the species' distribution. For example, diadromy is facultative (Russell 1990; Pender and Griffin 1996) and primary females (i.e. not derived from males) have been reported from slow growing but precocious populations in the northern Gulf of Carpentaria (Davis 1984).

Barramundi spawn in high-salinity reaches of estuaries and nearby coastal foreshores before and during the wet season (e.g. September to March), with peak spawning times varying between regions and years and in relation to lunar and tidal cycles (Dunstan 1959; Davis 1985; Garrett 1987; MacKinnon 1987; Russell 1990). Post-larval barramundi use estuarine wetlands as nursery habitats (Dunstan 1959; Russell and Garrett 1983, 1985; Davis 1985), departing these habitats at the end of the wet season (e.g. April; Russell and Garrett 1985). Where possible, juveniles migrate upstream into freshwater habitats during their first year (e.g. Dunstan 1959; Griffin 1987; Stuart and Mallen-Cooper 1999), otherwise juveniles remain in tidal creeks for approximately one year before dispersing into adjacent waters (Russell and Garrett 1988). Barramundi that have accessed freshwater habitats remain there until maturing several years later, then return to the estuary when flow conditions permit, to spawn alongside estuarine-resident fish (Grey 1987). Mature barramundi generally do not return to freshwater habitats in Australian populations (Davis 1987; Griffin 1987).

Sampling commercial catch

We sampled the commercial catch of barramundi for three consecutive spawning seasons (year-1 = 2000/2001; year-2 = 2001/2002; year-3 = 2002/2003). We sampled six times (twice each year/spawning season) during the weeks preceding and following the seasonal fishing closure for barramundi, which occurs from 1 November to 31 January. Sampling occurred at local seafood processors, who purchased most of the estuarine fish caught by commercial fishers in the region. We attempted to measure all barramundi (total length (TL) $\pm$ 10 mm) purchased by each of the seafood processors during the sampling period and to remove otoliths (sagittae) from as many of these fish as possible. We also identified approximately where each fish was caught, by questioning the processors or fishers. Only barramundi caught in the Fitzroy River estuary (including around Port Alma and the Narrows, see Fig. 1) were used in the present study. Sex of fish was not recorded, as the fish were 'cleaned' (i.e. gills and viscera removed) before arriving at the seafood processors.

Age estimation

Otoliths were blocked in resin, sectioned at 300 μm, then mounted on microscope slides. We viewed sections with a microscope using reflected light. In general, there is very clear differentiation between the slow (narrow, opaque, light) and fast (broad, translucent, dark) growth zones in barramundi otoliths from the Fitzroy River (Stuart and McKillup 2002). We counted the opaque increments and assigned the marginal increment to one of three categories: (*i*) 'new', when the opaque increment was on the margin; (*ii*) 'plus', when the opaque increment was separated from the margin by a narrow translucent increment; and (*iii*) 'due', when the distance from the outer opaque increment to the margin was almost equal to the width of the previous translucent increment.

Counts of opaque increments were converted to ages, taking into account the assessment of marginal increment and the date of capture. We assigned 1 January as the birthday of each fish, because the spawning season for barramundi extends from approximately October to March on the east coast of Queensland (Russell 1990). Therefore, all fish born during the same spawning season were assigned the same birthday and identified as belonging to the same year class. Once ages were estimated, age–length keys were constructed and used to convert length frequencies into age frequencies. Age–length keys and length–frequency distributions were constructed for each of the six sampling trips. A single age structure was constructed for each spawning season sampled (October plus February).

Our ability to estimate the absolute (cf. relative) age of individual barramundi was validated using fish with known ages from Lake Awoonga (three fish: one, three and four years old) and the Johnstone River (12 fish: two to eight years old; Andrew McDougall, Department of Natural Resources Mines and Energy, Queensland, unpublished data). Lake Awoonga is on the Boyne River less than 100 km south of Rockhampton, whereas the Johnstone River (latitude 17°32′S, 146°2′E) is ~800 km north-west of Rockhampton (Fig. 1). These fish had been tagged and stocked into the respective systems as small fingerlings. The otoliths used for validation were sectioned and read in the same manner as for other otoliths. Our estimates of age from otoliths matched the known ages of all 15 fish.

Estimating year-class strength (YCS)

We used the method described by Maceina (1997) to estimate YCS objectively from population age structure using catch-curve regressions (i.e. regression of the natural log of the number of fish in each year class against age). Deviation from an expected abundance of each year class, given its age and the catch-curve regression equation, is assumed to reflect variable recruitment. Therefore, residuals from the catch-curve regressions are indices of YCS, with large positive and negative residuals representing strong and weak year classes respectively.

Barramundi has minimum (580 mm) and maximum (1200 mm) legal size limits on the east coast of Queensland. Therefore, the size structure of the commercial catch is not representative of the whole population. To account for this potential bias, we restricted analyses to a range of age classes that were likely to be least biased by the restricted size structure. We selected age classes to include in analyses after we examined the size distribution of each age class in both October and February samples (pooled for all three years). The youngest age class we included was the youngest one for which >90% of the individuals measured were larger than the minimum size class of fish sampled (580–599 mm). This criterion was used as an approximate indication that most fish in this age class were likely to have reached the minimum legal size limit. Likewise, the oldest age class we included in our analyses was the oldest one for which >90% of the individuals we measured were smaller than the maximum size class of fish sampled (1180–1200 mm). This criterion was used as an approximate indication that most fish in this age class were unlikely to have exceeded the maximum legal size limit.

Relationships between YCS and fresh water flowing into the estuary

We investigated the relationship between YCS and freshwater flowing into the estuary by: (*i*) correlation analyses of YCS and freshwater flow variables (river flow and coastal rainfall, plus stocking); and (*ii*) best-subsets general linear modelling (GenStat 2002, Release 6.1, VSN International Ltd., Oxford) with year class abundance as the response and age, sample year, freshwater flow variables and stocking as independent variables. Age was forced in the model, as was sample year, because the abundance of individual age classes is not comparable between years. Significant models with three freshwater flow terms were reported. We examined serial autocorrelation of regression residuals using residual maximum likelihood (REML, GenStat 2002) to investigate whether there is evidence that recruitment success is autocorrelated (e.g. due to stock-recruitment relationships). The results showed no significant autocorrelations, thus standard general linear-modelling methods were used. The general linear models were used for data exploration and model screening. Ridge regression (GenStat 2002) was used to account for any lack of independence between freshwater flow variables (i.e. river flow and coastal rainfall) in the final models. This statistical method identifies and adjusts for observed levels of collinearity and provides adjusted regression coefficients that are the expected values had the X-variables been independent.

We used two variables as indices of fresh water flowing into the estuary: river flow (i.e. water flowing down the Fitzroy River and through the barrage); and coastal rainfall (i.e. rainfall in the catchment of the estuary itself and in catchments of creeks entering the river below the barrage). River flow and coastal rainfall were expressed as seasonal totals (i.e. total flow for the Fitzroy River and total rainfall, averaged across stations within the coastal region of the Fitzroy River estuary). We obtained river flow data from the Department of Natural Resources, Mines and Energy, Queensland and rainfall data from Rainman StreamFlow 4.3 (Clewett *et al*. 2003). River flow equalled gauged flow at the most downstream gauging station (i.e. at 'The Gap', 142.1 km Adopted Middle Thread Distance), minus the estimated downstream extraction. Seasons are defined as: spring (September to November), summer (December to February), autumn (March to May) and winter (June to August). Fish-stocking events were factored into analyses using the total number of barramundi fingerlings stocked in the Fitzroy River catchment per year between September and the following August. These totals did not include fish stocked into upstream impoundments that had not overflowed since being stocked. River flow, rainfall and stocking data were transformed ($\log_{10} + 1$) to normalise data and stabilise variances.

Assumptions

We have made several assumptions in using age structure of the commercial catch to estimate YCS and recruitment variability.

(1) Age structure is determined mainly by recruitment

The main assumption of using age structure of the adult population to infer patterns in recruitment of juvenile fish is that YCS is determined during the first year of life. We assume that strong and weak year classes persist through time, but acknowledge that density-dependent processes, such as competition, predation and fishing pressure, might dampen the variability in YCS after the recruitment of juveniles (e.g. Maceina 1997; Rothschild 2000). We validate this assumption partially by sampling for three consecutive years, thus confirming that patterns in YCS are consistent through time. If YCS is not related to variability in recruitment of juvenile fish, then our method will be unable to detect factors that have a major influence on recruitment variability.

(2) Migration rates between estuaries are low

Migration rates of barramundi into and out of the study region are assumed to be low, so that patterns observed in the population age structure (i.e. YCS) can be related to local environmental conditions. In Papua New Guinea, barramundi undergo extensive migrations to a single major spawning ground (Moore 1982). However, in Australia, most individuals remain within a specified region (Russell and Garrett 1985; Davis 1986; Salini and Shaklee 1988; Keenan 1994) and tagging data from the Fitzroy River region support the assumption that migration rates are low (Australian National Sportfishing Association, Infofish Services, Rockhampton, unpublished data).

(3) Fish stocking does not bias the results

Stocking of fingerlings into open systems potentially compromises the ability to detect variability in natural recruitment. Barramundi have been stocked in the Fitzroy River catchment since February 1990 to enhance recreational fisheries in freshwater impoundments. Natural upstream migration of barramundi to many of these areas has been reduced by the construction of dams and weirs. However, recaptures of tagged fish have demonstrated that downstream migration of fish from many stocked impoundments to the estuary can occur when floods cause these impoundments to overflow (Australian National Sportfishing Association, Infofish Services, Rockhampton, unpublished data). Data on stocking rates were obtained from the Department of Primary Industries and Fisheries, Queensland, and have been included in analyses in the same way as river flow and coastal rainfall variables. Some interpretation of these data was required so that only fish stocked into impoundments that have overflowed were included.

(4) Age structure of the adult population can be estimated accurately

We assume that we have minimised, or at least taken into account, biased sampling of the Fitzroy River barramundi population. We chose to use fishery-dependent sampling of the estuarine population, by measuring fish and collecting otoliths at seafood processors. Some of the factors that potentially compromise our ability to collect representative samples of the population using commercial catches include: (*i*) the diadromous life cycle of barramundi (commercial fishing only occurs in saltwater regions); (*ii*) the size-selective fishing method (gill-nets); and (*iii*) the legal size limits on the species (580–1200 mm). However, barramundi spawn in marine environments, thus they attempt to reach, and then remain in, estuaries after they mature. Potential bias in our estimates of age structure owing to size selectivity of gill-netting is reduced because age structure is more important in our analyses than size structure, and there is considerable variability in age-at-size. Furthermore, a range of mesh sizes (15.2–20.3 cm) is used in the commercial fishery. Finally, our analyses are limited to a subset of available age classes to account for the youngest and oldest fish in the population being underrepresented in commercial catches because of minimum and maximum legal size limits.

Results

Sampling commercial catch

Between October 2000 and February 2003, we measured a total of 1898 barramundi that had been caught within the Fitzroy River estuary (Table 1). The barramundi ranged from the minimum legal size limit (580 mm) to the maximum legal size limit (1200 mm) for the species (Fig. 2).

Age estimation

There was very clear differentiation between fast- and slow-growth zones on barramundi otoliths from the Fitzroy River estuary, as found by Stuart and McKillup (2002). Opaque (light, narrow) increments were visible on the margin of most otoliths collected in October, but were rarely on the margin of otoliths collected in February (Table 2), suggesting that increments form by October. Therefore, when estimating the age of a fish collected in October, and when an increment was not visible on or near the margin of the otolith, we assumed that one should have been present. Consequently, an extra year was added to the estimated ages of 46 fish that were caught in October but had an otolith increment classed as 'due'.

Table 1. Number of barramundi measured and pairs of otoliths collected each year at commercial seafood processors

Year-1 = October 2000 + February 2001; year-2 = October 2001 + February 2002; year-3 = October 2002 + February 2003

Year	No. measured	No. otoliths collected
1	650	567
2	643	323
3	605	443
	Total = 1898	Total = 1333

Estimates of age of sampled fish ranged from two to 32 years old. There was substantial variation in the length of fish within age classes and the age of fish within length classes (Fig. 3). For example, fish between 900 and 950 mm TL ranged from three to 11 years old, and five-year-old fish ranged from 580 to 1030 mm.

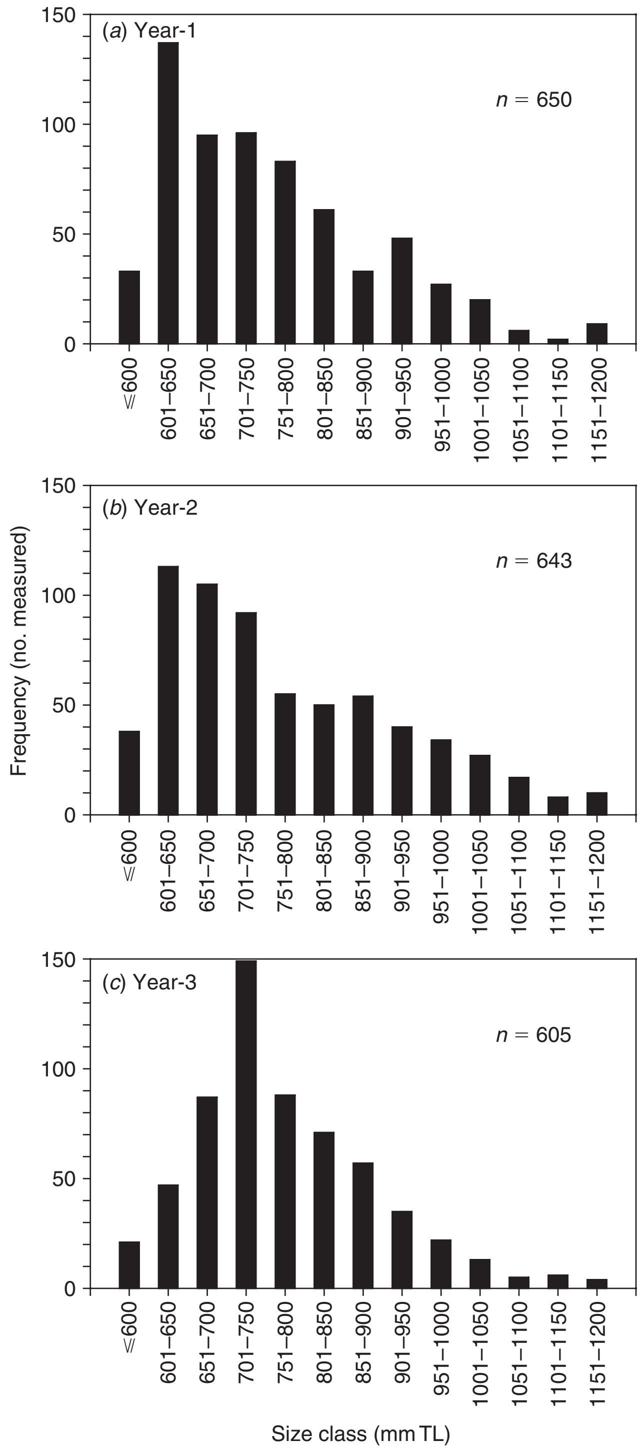

Fig. 2. Size–frequency distribution of barramundi sampled from commercial catches in the Fitzroy River estuary in three successive years. (*a*) Year-1 (October 2000 + February 2001), (*b*) year-2 (October 2001 + February 2002) and (*c*) year-3 (October 2002 + February 2003).

The size and age structure of sampled fish were examined to determine which age classes to include in the analysis. At the lower end of the size and age ranges, 92.5% of two-year-old fish were larger than the smallest size class (580–599 mm, with 580 mm being the minimum legal size), but only three of these were caught during October trips. Therefore, we believed this age class had not recruited sufficiently to the commercial fishery. Of the three-year-old fish, 96.1% were larger than the 580–599 mm size class and three year olds were common in October and February trips, so we decided this age class was the youngest one that should be included in our analyses. At the upper end of the size and age ranges, the youngest fish to have reached the maximum legal size limit was 10 years old, although most 10-year-old fish were smaller than 1090 mm. Similarly, most 11-year-old fish were smaller than 1080 mm, with 93.3% being smaller than the largest 20-mm size class (1180–1200 mm). Although most 12-year-old fish were smaller than 1060 mm, 28.6% were in the 1180–1200-mm size class. Therefore, we decided that the 11-year-old age class was the oldest one that should be included in our analyses.

Age structure

There was a consistent change in the age structure of samples from year-1 to year-3 (Fig. 4). In year-1, the five-year-old age class was the most abundant, especially compared with the six-, seven- and eight-year-old age classes. The nine- and ten-year-old age classes were also more abundant than the six-, seven- and eight-year-old age classes. A similar pattern was observed in year-2 and year-3, except that it had progressed by one and two years respectively. A notable feature in year-2 was that the three-year-old age class was the most abundant, accounting for >40% of the sample. This cohort

Table 2. Results of marginal increment assessment for barramundi in the Fitzroy River region

Marginal increments defined as: 'new', when the opaque increment is on the margin; 'plus', when the opaque increment was separated from the margin by a narrow translucent increment; 'due', when the distance from the outer opaque increment to the margin was almost equal to the width of the previous translucent increment

	Sample time	Marginal increment			Total
		New	Plus	Due	
Year-1					
	October 2000	154			154
	February 2001	2	412		414
Year-2					
	October 2001	85		44	129
	February 2002	1	192	3	196
Year-3					
	October 2002	122		2	124
	February 2003		319		319

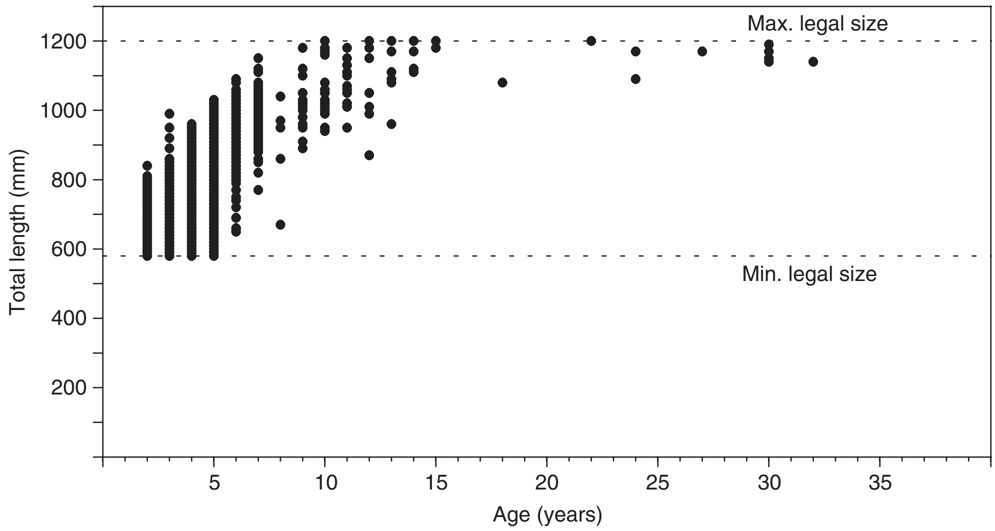

Fig. 3. Length-at-age of barramundi sampled from commercial catch taken from the Fitzroy River estuary. Dashed lines indicate maximum and minimum legal size limits for this species.

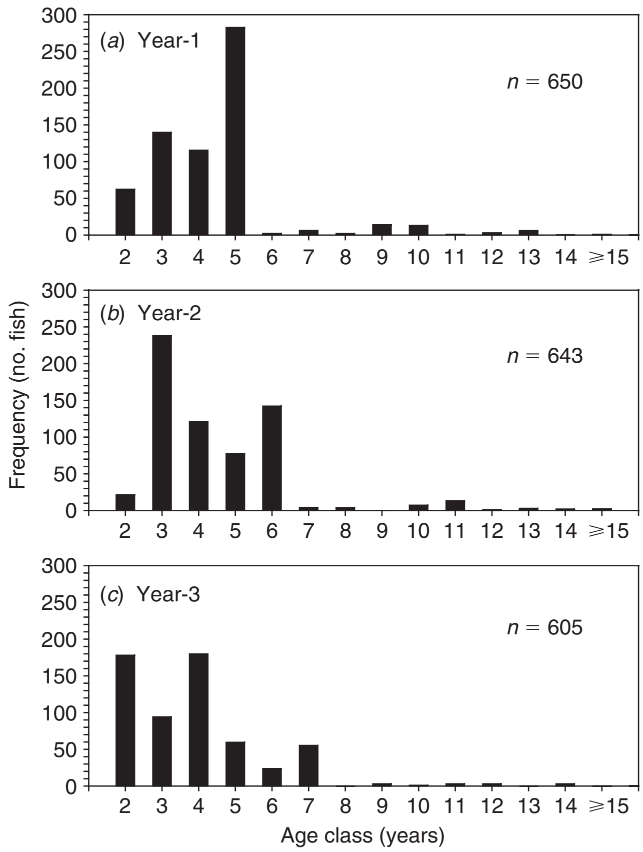

Fig. 4. Age–frequency distribution of barramundi sampled from commercial catches in the Fitzroy River estuary in three successive years. (*a*) Year-1 (October 2000 + February 2001), (*b*) Year-2 (October 2001 + February 2002) and (*c*) Year-3 (October 2002 + February 2003).

of fish remained abundant in year-3 (i.e. as four-year-old age class), when it was joined by the two-year-old age class as the second most abundant age class.

Year-class strength (YCS)

The consistency in age structure across the three years of sampling is reflected in the estimates of YCS using standardised residuals from the catch-curve regressions (Fig. 5). The most notable features were that the strength of three year classes, 1991, 1992 and 1996, was consistently strong (i.e. large positive residuals), whereas strength of three other year classes, 1993, 1994 and 1995, was consistently identified as weak (i.e. large negative residuals). Strength of the 1990, 1997 and 1998 year classes could not be classed as strong or weak because they had relatively small residuals. The 1999 year class had a small positive residual in year-2 (when fish were three years old) and a large positive residual in year-3 (when fish were four years old). The 2000 year class had a large negative residual in year-3.

Relationships between YCS and fresh water flowing into the estuary

Not surprisingly, patterns in river flow reflect those exhibited by coastal rainfall: river flow during spring, summer and autumn was significantly correlated with coastal rainfall during the same period ($r = 0.62$, 0.81 and 0.60 respectively, $P < 0.05$, $n = 11$), though not in winter. These results suggest that significant correlations between YCS and one index of freshwater flow (i.e. river flow) will also be found for the other (i.e. coastal rainfall). This was the case with both

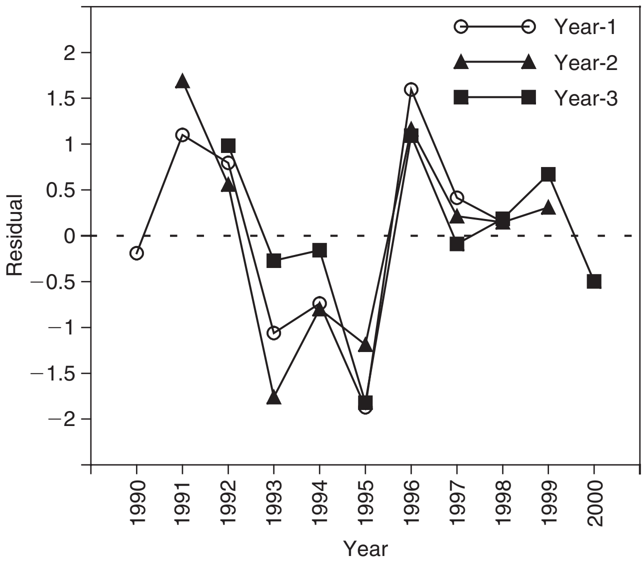

Fig. 5. Variation in standardised residuals from catch-curve regressions ($\log_e$ abundance against age) of barramundi sampled from commercial catches in the Fitzroy River estuary for three successive years. ○, Year-1 (October 2000 + February 2001); ▲, year-2 (October 2001 + February 2002); ■, year-3 (October 2002 + February 2003).

river flow and coastal rainfall in summer being significantly correlated with YCS (i.e. the residuals from the catch-curve regressions) (Fig. 6). However, spring river flow, but not coastal rainfall, was correlated with YCS. The remaining variables (i.e. river flow and coastal rainfall during autumn and winter, and annual stocking rate) were not significantly correlated with YCS.

Best-subsets general linear modelling provided two alternate significant models, each with three terms in addition to the forced-age and sample-year terms. The model with only age and sample year explained 51.7% of the variation in the abundance of age classes. For the ridge regression adjustments to the best final models, Draper and Smith's (1998) optimal k was estimated at between 0.1 and 0.2 for the two final models. Also, considering the ridge traces and indices of stability (Vinod 1976), a value of $k = 0.1$ was chosen as the most appropriate overall value. This indicates a 'minor' adjustment of the regression equation, where $k = 0$ equates to a standard GLM solution and $k = 1$ gives the maximum adjustment. Parameter estimates for significant freshwater flow terms in the best final models were all positive in direction. The three additional terms in the first significant model were summer river flow, stocking and autumn rainfall (all with $P \leq 0.001$; overall $R^2 = 91.5\%$). This model thus explained 82.4% of the residual variation from the age and sample-year model. In the second significant model, the three additional terms were summer coastal rainfall ($P \leq 0.001$), spring river flow ($P \leq 0.001$) and winter river flow ($P = 0.011$) (overall $R^2 = 90.6\%$), explaining 80.5% of

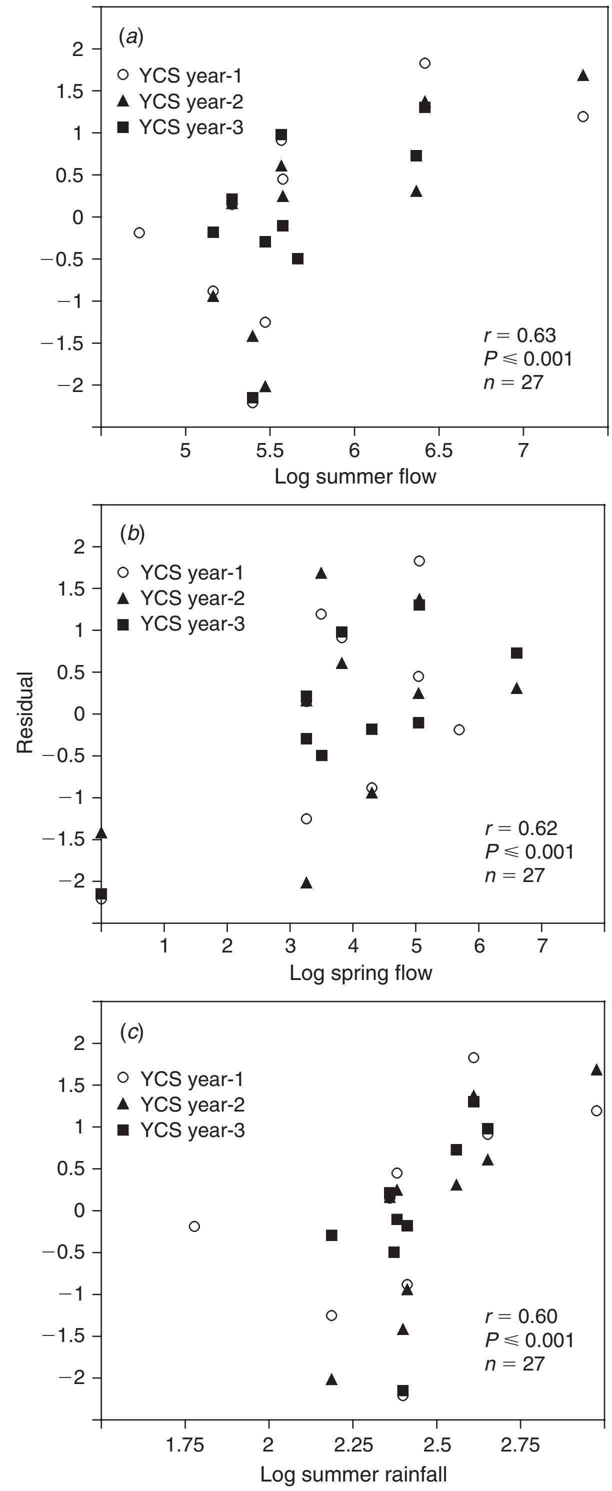

Fig. 6. Relationships between residuals from catch-curve regressions ($\log_e$ abundance against age) of barramundi sampled from commercial catches in the Fitzroy River estuary for three successive years and (*a*) $\log_{10}$-transformed summer river flow, (*b*) $\log_{10}$-transformed spring river-flow and (*c*) $\log_{10}$-transformed summer rainfall. ○, Year-1 (October 2000 + February 2001); ▲, year-2 (October 2001 + February 2002); ■, year-3 (October 2002 + February 2003). Correlation test results are included on each graph.

the variation in the abundance of age classes not explained by age and sample year.

Discussion

The age structure of commercially caught barramundi in the Fitzroy River estuary, which we examined for three consecutive years, demonstrated that strong and weak year classes are detectable and persistent in the adult population. The relative strengths of these year classes were significantly correlated with the amount of fresh water flowing into the estuary, particularly during spring and summer. Some of this fresh water came from rainfall occurring in close proximity to the estuary (i.e. coastal rainfall resulting in flows in small creeks flowing directly into the estuary), whereas some came from rainfall throughout the Fitzroy River catchment (i.e. rainfall resulting in flows in the Fitzroy River).

In general, long-lived species, which have numerous age classes in the population, are buffered against vast recruitment-based variation in stock size, unless there is a series of strong or weak year classes (McGlennon *et al*. 2000). However, the large variability in YCS we observed, and persistence of strong and weak year classes in the population through time, suggests that recruitment variability has the potential to influence adult stock size. Therefore, our results support the suggestion of Williams (2002) that commercial catches of barramundi can be highest in years when very strong year classes become vulnerable to capture in the fishery several years after they have been born. Knowledge of this relationship should be useful to fisheries managers because it can be included in stock-assessment models (Shepherd *et al*. 1984).

The significant correlation between spring and summer freshwater flows and year-class strength supports the suggestion that flows at that time of year affect the abundance and survival of very young barramundi (i.e. juvenile recruitment), which occur in estuarine habitats at that time (Dunstan 1959; Russell and Garrett 1983, 1985; Davis 1985). There are at least three potential explanations (i.e. causal mechanisms) for this correlation, based on what is known about the life cycle of barramundi from studies in northern Australia. The mechanisms are not mutually exclusive and it is unlikely that they represent the only mechanisms by which freshwater flows affect survival of juvenile barramundi.

Dunstan (1959) suggested that the spawning population of barramundi in marine waters might be greatly reduced below its potential in the absence of mature female fish that have been living in fresh water. This explanation is based on the beliefs that egg production is substantially higher in years when floodwaters release land-locked fish, and that increased egg production results in increased numbers of juvenile fish. However, according to the generalised life cycle of barramundi, most fish migrating from freshwater habitats are likely to be males. It is uncertain whether enough mature females arrive from freshwater habitats to increase egg production greatly.

The second explanation for a link between spring and summer flows and recruitment of barramundi in the Fitzroy River region is that survival of barramundi during the first months of life is higher in wet years than dry years. In other regions of the species' distribution, larvae and very young juveniles have been observed in ephemeral supralittoral nursery habitats in close proximity to spawning areas, such as coastal swamps and lagoons and supralittoral pools on salt pans (Dunstan 1959; Moore 1982; Russell and Garrett 1983, 1985; Davis 1985; Griffin 1987). The spatial and temporal extent (and probably productivity) of many of these nursery habitats is affected by the amount of freshwater runoff, and access to and from them is dependent on high seasonal tides and/or freshwater flows (Russell and Garrett 1983; Davis 1985; Griffin 1987). The locations of habitats used by very small barramundi (e.g. <50 mm TL) in the Fitzroy River region are currently unknown. However, they could include the substantial supralittoral habitats that occur close to the mouth of the estuary (Dunstan 1959; Long and McKinnon 2002). It is possible that high coastal rainfall and freshwater flows in the Fitzroy River enhance survival of the early life-history stages of barramundi by generating and improving access (e.g. frequency, extent and duration of access routes) to supralittoral nursery areas, increasing their productivity and carrying capacity, and/or increasing their suitability in some other way (e.g. physicochemical characteristics).

The third explanation is that survival of juvenile barramundi is enhanced in wet years at some stage after they have departed wetland nursery habitats (many of which are ephemeral), which typically occurs at the end of the wet season (Russell and Garrett 1983, 1985). Although individual barramundi can complete their entire life cycle in estuaries and coastal waters (Griffin 1987; Russell 1990), it is possible that survival rates of juvenile barramundi are higher if they access freshwater habitats, where they remain until sexual maturity (Griffin 1987; Grey 1987). In the Fitzroy River, juvenile barramundi, mainly between 250 and 400 mm in length and approximately one year old, have been reported migrating upstream using the fishway on the tidal barrage (Stuart and Mallen-Cooper 1999; Stuart and McKillup 2002). However, access to, and suitable conditions within, other significant off-stream freshwater habitats (e.g. swamps, lagoons and billabongs) up and downstream of the barrage, might be restricted to times of high river flows or flooding rain. For the results of our study (i.e. that YCS is related to spring and summer flows) to support this suggestion, then large numbers of juvenile barramundi in the Fitzroy River region would either have to depart the wetland nursery habitats before the end of the wet season (i.e. autumn) or not have entered those habitats in the first place.

In addition to the significant correlations between YCS and fresh water flowing into the estuary during spring and summer, the results of multiple regression suggested that other factors might also have positive effects on YCS, such as stocking, coastal rain during autumn and river flow during winter. The potential positive influence of stocking on YCS is obvious. However, it should be noted that stocking was not significantly correlated with YCS in the absence of other factors (i.e. summer flow and autumn rain). This may be because natural recruitment outweighs the contribution of stocking to the population, particularly in 'good' years, or because the same conditions that affect survival of naturally recruited fish might affect survival of stocked fish (e.g. spring and summer flows). The occurrence of autumn rain and winter river-flow variables as significant terms in the multiple regression models suggest these factors may also be important for the survival of juvenile barramundi.

Method of estimating YCS

By using the method of Maceina (1997) to estimate YCS we have been able to objectively, quickly and cheaply obtain information on large-scale variability in recruitment for an estuarine species of fish in northern Australia. Several year classes were consistently identified as strong or weak in samples of barramundi from three consecutive years. A minor exception to the consistent pattern observed was the 1999 year class, which appeared strong in the year-3 sample, but not in the year-2 sample. The reasons for this (assuming that it was in fact a strong year class) could have been that it had not become sufficiently vulnerable to the fishery until year-3 (i.e. when the fish were four years old). Based on the size distribution of age classes, it appeared that most three year olds should be larger than the minimum legal size. However, vulnerability is not solely related to size, as commercial fishing is not permitted in the freshwater habitats, where young barramundi occur. The increase in relative YCS of the 1999 year class in year-3 could, therefore, correspond with the increase in vulnerability of the year class following departure of large numbers of fish from freshwater habitats.

The ability to sample a species adequately is a potential problem for a study estimating relative rates of annual recruitment, especially if the study measures the abundance of a single life-history stage. The distribution of very small barramundi (e.g. <50 mm TL) is not known in the Fitzroy River region, and larger juvenile fish occur in a wide variety of saltwater and freshwater habitats spread throughout the catchment. Thus, representative sampling of the juvenile barramundi population would be difficult. In contrast, mature adult barramundi depart the freshwater habitats when conditions permit and return to the estuary to spawn. Thus the estuarine population consists of a mixture of fish that spent their juvenile stage in freshwater habitats and those that had always been in the estuary. Sampling the adult life-history stage of barramundi in the estuary represents a convenient method for comparing the relative abundance of numerous year classes.

In general, real-time research studies that measure annual recruitment directly (i.e. abundance of individual year classes) have a low probability of successfully and quickly detecting links between environmental variability and recruitment because of climatic unpredictability and, thus, inadvertently having a study period in which no obvious relationships are evident (Walters and Collie 1988). For example, the Fitzroy River is situated in the dry tropics and, as such, it is uncertain that a short time frame (e.g. three years) would contain a balance of 'wet' and 'dry' years. However, there were several 'wet' years during the decade before the commencement of this study and these were interspersed with 'dry' years. There was also variability in the timing of high river flows and coastal rainfall. If there is a close relationship between fresh water flowing into the estuary and recruitment of barramundi, then the recent environmental variability should have resulted in variable recruitment and, thus, detectably strong and weak year classes. A simple method to assess the strength of many year classes concurrently, such as the one used in this study, could prove useful in circumstances where long periods of time are not available to investigate relationships between environmental conditions and recruitment in more detail (e.g. because of limited resources or urgency for results).

Despite these advantages (e.g. in terms of efficiency and expediency), the main disadvantage of not measuring recruitment strength directly (e.g. abundance of larvae, post-larvae and young juveniles) is that the causal mechanisms for the relationship between the fresh water flowing into the estuary and the strength of the year class remain unproven. Our results support hypotheses based on known life-history information of barramundi pieced together from different regions in northern Australia. However, several questions remain unanswered. For example, the life-history stage at which YCS is determined is not known and nursery habitats used by some of the early life-history stages (i.e. larval and post-larval) have not yet been located in the Fitzroy River region. Therefore, the relative effects on estuarine nursery habitats of freshwater flows originating in the upper Fitzroy River, and those resulting from localised coastal rainfall, cannot as yet be differentiated because of the correlation between these two indices of freshwater flow. The exact mechanism(s) by which freshwater flows affect the recruitment of barramundi remain speculative, as do quantitative estimates of the freshwater requirements of the species (e.g. timings, duration and magnitude). However, it is unlikely that management of freshwater resources can wait until full knowledge of the mechanisms behind the relationship between freshwater flow and juvenile recruitment is understood. Management of freshwater resources will by necessity be based on best available knowledge, even if it is incomplete or speculative.

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