FRESHWATER FLOWS AFFECT THE YEAR-CLASS STRENGTH OF BARRAMUNDI *LATES CALCARIFER* IN THE FITZROY RIVER ESTUARY, CENTRAL QUEENSLAND.

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The age-structure of the commercial catch of barramundi in the Fitzroy River estuary, central Queensland, was examined over five consecutive years and used to estimate year-class strength (= index of recruitment). Barramundi year-class strength fluctuated and was significantly and positively correlated with freshwater flow and coastal rainfall in spring and summer. General linear models were used to identify relationships between year-class strength and freshwater variables, and explained between 85 and 90% of the variation in barramundi year-class strength. The results provide further evidence that recruitment variation in barramundi: (i) persists over time; and (ii) is significantly correlated with the volume to freshwater flowing into the estuary. We reviewed the evidence in support of the three causal mechanisms currently proposed to explain the relationship between year-class strength and juvenile barramundi recruitment; and propose an additional mechanism, that of enhanced growth rates and thus increased survival of young-of-the-year. Freshwater flow is an important driver of barramundi recruitment, and reduction in flow, through water abstraction or climate change, will potentially reduce barramundi stock size available for human harvest. As such, fishery stock assessments for barramundi should explicitly consider the impacts of variable flow on annual recruitment and stock dynamics. □ *environmental flows, fish recruitment, otoliths*.

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Received: 28 April 2010; Revised: 5 July 2010; Accepted: 6 July 2010

INTRODUCTION

Within Queensland, freshwater resources are managed under Queensland State law (Queensland Water Act, 2000), and involve balancing the water needs associated with human demand against the water needs of the environment. Allocations for the environment, termed 'environmental flows' (Tharme, 2003) are aimed at protecting the health of natural ecosystems while providing security of supply to water users. Natural ecosystems include freshwater sections of rivers (including riparian habitats) as well as the downstream estuarine section, often considered to be the "End-of-System" (Jayasuriya, 2004; Lester & Fairweather, 2009).

Freshwater flowing into estuaries is a key factor defining an estuary. However, how much water is required to sustain estuarine biota and the impact of changing freshwater flows is not fully understood. Methods to determine the freshwater requirements of estuaries are in their infancy (Estevez, 2002), with one approach focusing on relationships between fishery catches and measures of freshwater inflow. Estuarine species and communities often respond positively to increased river flow (or rainfall), with increased catches of prawns, crabs and fish (Drinkwater & Frank, 1994; Loneragan & Bunn, 1999; Robins et al., 2005). There are three main proposed causal mechanisms linking river flow to increased fisheries production: (i) that freshwater flows enhance the overall biological productivity of estuaries through nutrient input; (ii) that freshwater flows alter the accessibility of nursery habitats and improve the recruitment and abundance of estuarine species; and (iii) that freshwater flows may affect catch rates of selected species by triggering behavioural responses such as movement and spawning (Copeland, 1966; Aleem, 1972; Peters, 1982; Drinkwater, 1986; Drinkwater & Frank, 1994; Loneragan & Bunn, 1999; Gillanders & Kingsford, 2002). It is likely that all three mechanisms occur, but to what extent, for which species and how they interact to influence fisheries catches is unclear.

Barramundi (*Lates* calcarifer) is an important species in Queensland and northern Australia supporting recreational and commercial fisheries of considerable value (Kailola et al., 1993; Williams, 2002). Barramundi is a long-lived, fast-growing species and has a complex and variable life-history (Dunstan, 1959; Moore, 1982; Davis, 1985; Russell & Garrett, 1985; Griffin, 1987). In Australia, catadromy in barramundi is not obligatory (Pender & Griffin, 1996) with only a proportion of the population accessing freshwater habitats for some part of their life e.g. 60% in the Fitzroy River population (Milton et al., 2008). The population dynamics of barramundi are highly responsive to river flow. Barramundi recruitment depends on local spawning and is significantly and positively related to rainfall or river flow (Staunton-Smith et al., 2004), whilst catch is significantly correlated to lagged river flow (Robins et al., 2005; Balston, 2009) or rainfall (Meynecke et al., 2006). Barramundi growth rates vary both regionally (Davis, 1987), and seasonally (Xiao, 1999; 2000), with growth rates in all seasons significantly and positively influenced by river flow, provided that flow reaches critical thresholds (Robins et al., 2006).

We report here on the results of a 5-year study into the influence of freshwater flows on the recruitment patterns of barramundi in the Fitzroy River estuary of central Queensland and compare the findings with the results of earlier work on recruitment patterns to ensure that hypotheses and standing results from 3-years research (Staunton-Smith et al., 2004) were consistent with those from the current 5-years research. Research on the consistency of findings over time is an important, but often neglected aspect of science (Underwood, 1997). In addition, we reviewed evidence supporting the proposed causal mechanisms linking year-class strength and juvenile recruitment; and propose an additional mechanism i.e., enhanced growth rates and thus increased survival of young-of-the-year barramundi.

MATERIALS AND METHODS

SAMPLING THE COMMERCIAL CATCH

The commercial barramundi catch of the Fitzroy River estuary (c. 23°23’S; 150°28’E) was sampled twice per year (in October and the subsequent February) for five consecutive years, where year-1 = October 2000 + February 2001; year-2 = October 2001 + February 2002; year-3 = October 2002 + February 2003; year-4 = October 2003 + February 2004; and year-5 = October 2004 + February 2005. Sampling occurred at local seafood processors who purchased most of the estuarine fish caught in the region. All available barramundi were measured for total length (TL ± 10 mm) and sagital otoliths collected from as many individuals as time permitted. The capture location of each fish was determined by questioning the seafood processors (or commercial fisher when available) and only those barramundi caught in the Fitzroy River estuary (including around Port Alma and the Narrows), were used in the present study (as per Staunton-Smith et al., 2004).

FIG. 1. Transverse section (300 µm) of a sagital otolith from a barramundi sampled from the commercial catch of the Fitzroy River estuary, viewed with reflected light. Opaque bands represent annuli. Estimated age = 6 years.

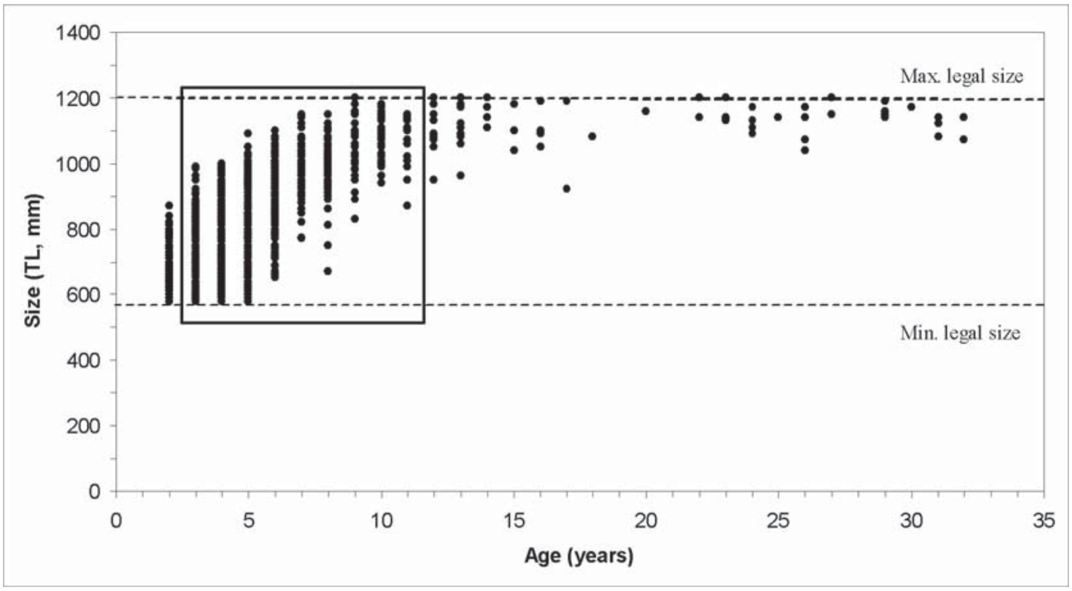

FIG. 2. Size-at-age plots for barramundi sampled over five years from the commercial net fishery of the Fitzroy River estuary (n=2112). (TL = total length). Box indicates ages-classes used in the calculation of barramundi year-class strength.

AGE ESTIMATION

Each barramundi otolith was blocked in resin, sectioned at 300 µm, mounted on microscope slides and viewed through a microscope using reflected light. Barramundi from the Fitzroy River region have very clear differentiation between sequential opaque and translucent bands on the otoliths (Fig. 1), which are generally assumed to be representative of slow and fast growth respectively (Campana & Neilson, 1985). The age of an individual was estimated by counting the number of opaque bands on the sectioned otolith (Stuart & McKillup, 2002; Staunton-Smith et al., 2004). Annual age-length keys were constructed and used to convert length-frequency distributions into a single age-structure of the barramundi population resident in the Fitzroy River estuary for each sampling year.

ESTIMATING YEAR-CLASS STRENGTH (YCS)

The commercial net fishery for barramundi selectively harvests fish between 580 mm (minimum legal size) and 1200 mm (maximum legal size). Therefore, the size structure of the commercial catch is not representative of the whole population. To eliminate the potential bias in our analyses because of net (and therefore size) selectivity, we restricted our analyses to fish aged between three- and eleven-year-olds, as >90% of these age-classes are considered to be sampled representatively by the commercial fishery (Staunton-Smith et al., 2004). Year-class strength (YCS) was estimated using deviations from annual catch-curve regressions (Maceina, 1997), where large positive and negative residuals represent strong and weak year-classes respectively.

ANALYSIS OF YCS WITH FRESHWATER FLOW

The relationship between YCS and freshwater flowing into the estuary was examined using: (i) correlation; and (ii) all sub-sets general linear modelling (GenStat, 2008), with year-class strength as the response variable, age and sample year as forced variables, and freshwater flow, coastal rainfall and stocking as independent variables. All sub-sets GLM calculates all possible combinations of forced and independent variables to identify a number of alternative regression models that can be evaluated by their explanatory power (adjusted R^2) and biological plausibility. Daily freshwater flow (m^3sec^{-1}) were obtained from the Department of Environment and Resource Management (DERM), where flow to the estuary equalled gauged flow at the most downstream gauging station (i.e., 'The Gap', 142.1km Adopted Middle Thread Distance), minus the estimated extractive use provided by DERM and Fitzroy River Water as per Robins et al. (2005). Monthly coastal rainfall was averaged for the nine rainfall stations that were within 50 km of the coast and on the seaward side of the coastal mountain ranges in the Fitzroy River region. Rainfall data was sourced from Rainman StreamFlow 4.3™ (Clewett et al., 2003). Coastal rainfall was included in analyses (in addition to freshwater flow) because large floods can flow into the Fitzroy River estuary as a consequence of high rainfall events in the upper sub-catchments of the vast Fitzroy River catchment (142537km^{2}) without the occurrence of coastal rainfall. Flow and rainfall were aggregated into seasonal totals, where spring = September to November, summer = December to February, autumn = March to May and winter = June to August. A spawning season aggregate of flow or rainfall (i.e., September to February) was also included in the analyses. Barramundi fingerlings are stocked into impoundments and lagoons of the Fitzroy River and contribute to the estuarine catch. Therefore, stocking is a potential contributor to barramundi year-class strength in this catchment and needed to be factored into analyses. We used the total number of barramundi fingerlings stocked in the Fitzroy River catchment per year between September and the following August as an index of stocking and only considered fish stocked into areas that had overflowed/flooded since stocked with fingerlings. Flow, rainfall and stocking data were transformed ($\log_{10}$ +1) prior to analyses, to normalise data and stabilise variances.

RESULTS AND DISCUSSION

A total of 2690 barramundi were measured and 2112 were aged using otoliths over the five consecutive years of sampling the commercial net fishery catch in the Fitzroy River estuary.

AGE AND LENGTH OF SAMPLED FISH

Barramundi ranged in age from two-years-old to 32-years-old, with 8.3% aged as two-year-olds, 88.4% aged between three- and eleven-years-old, 2.0% aged between 12- and 20-years-old, and 1.3% aged greater than 20-years-old. Sampled barramundi ranged in length from the minimum legal size (580 mm) to the maximum legal size (1200 mm). Size-at-age was highly variable for barramundi, particularly for fish aged between two and ten years (Fig. 2). This variability means that size was not a reliable indicator of age for barramundi, and is consistent with variable growth of individuals, depending on the genetic and environmental conditions to which individuals are exposed (Morita & Morita, 2002; Robins et al., 2006).

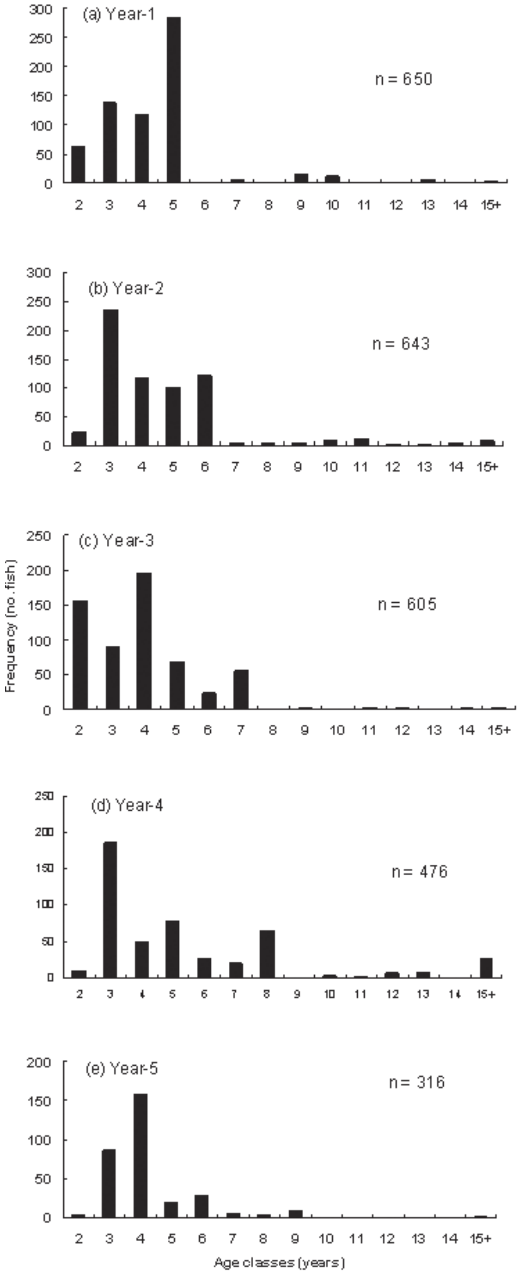

FIG. 3. Age-frequency distribution of barramundi sampled from commercial net catches in the Fitzroy River estuary for five consecutive years. (a) Year-1 (October 2000 + February 2001), (b) Year-2 (October 2001 + February 2002), (c) Year-3 (October 2002 + February 2003), (d) Year-4 (October 2003 + February 2004), and (e) Year-5 (October 2004 + February 2005).

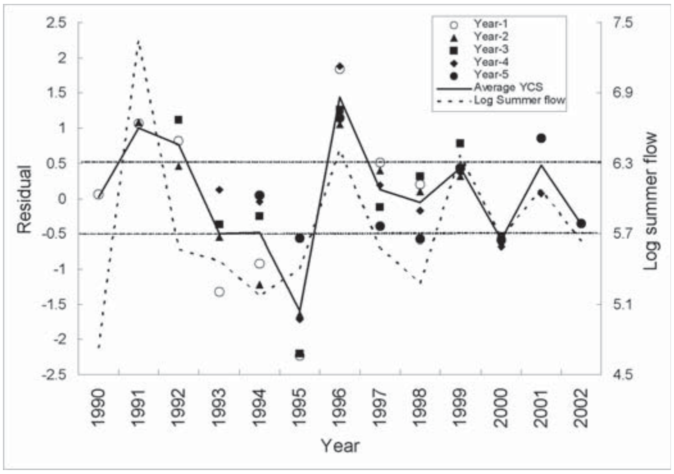

FIG. 4. Residuals from catch-curve regressions of barramundi sampled from commercial net catches in the Fitzroy River estuary for five consecutive years against summer freshwater flows. Year-1 (October 2000 + February 2001), Year-2 (October 2001 + February 2002), Year-3 (October 2002 + February 2003), Year-4 (October 2003 + February 2004), Year-5 (October 2004 + February 2005), solid line (—) = average year-class strength, dashed line = $\log_{10}$ summer flow.

AGE-STRUCTURE

There was a systematic change in the age-structure of the catch over the five years sampled. Of note, was the presence of strong year-classes that could easily be followed through the annual age-structures. For example, in sample year-1, the five-year-old age-class was 'strong', and could be seen as the six-year-olds in sample year-2, seven-year-olds in sample year-3, eight-year-olds in sample year-4 and nine-year-olds in sample year-5 (Fig. 3). Another strong cohort was the 2 year-old age-class in sample year-3. There were also 'weak' year-classes, whose presence in the catch was persistently 'weak' in the five sample years (i.e., the six-, seven- and eight-year old age-classes from year-1).

YEAR-CLASS STRENGTH

The standardised residuals from the catch-curve regressions were used to provide an objective index of the relative year-class strength (YCS) of barramundi. Year-classes 'born' in 1991, 1992 and 1996 had large, positive residuals, indicating strong recruitment, whilst those 'born' in 1995 and 2000 had large, negative residuals, indicative of weak recruitment (Fig. 4). The 2001 year-class had only two data points (and thus estimates of YCS), both of which were positive, but only one could be classed as indicative of strong recruitment i.e., a catch curve residual of 0.86 from the year-5 sample (Fig. 4). Of the remaining year-classes, 1990, 1997 and 1999 had small, positive residuals (i.e., 0.0 to +0.5) while 1993, 1994, 1998 and 2002 had small, negative residuals

TABLE 1. Product-moment correlation coefficients (r) between estimated year-class strength (YCS) and freshwater flow and rainfall variables for barramundi in the Fitzroy River estuary, (n=45).

	Barramundi YCS
Annual flow	0.55***
Annual rain	0.67***
Spawning season[A] flow	0.61***
Spawning season rain	0.63***
Spring flow	0.66***
Spring rain	0.17
Summer flow	0.60***
Summer rain	0.50**
Autumn flow	0.16
Autumn rain	0.09
Winter flow	-0.01
Winter rain	-0.24
Stocking	0.37*

*= $P<0.05$, ** = $P<0.01$, *** =$P<0.001$.
[A] Spawning season = spring + summer
(i.e., September to February inclusive)

(i.e., 0.0 to -0.5) and thus could not be classified as either 'strong' or 'weak' (Fig. 4). These results were consistent with those previously reported for all but the 1993 and 1994 year-classes (Staunton-Smith et al., 2004), and confirm the preliminary estimate of Staunton-Smith et al. (2004) of the 2000 year-class as 'weak' (i.e., large negative residual). Previously, the 1993 and 1994 year-classes had large, negative residuals (two of three estimates) and were therefore classified as having 'weak' recruitment (Staunton-Smith et al., 1994). The present results also concur with a smaller, localised study on fish usage of the Fitzroy River barrage (Stuart & Mallen-Cooper, 1999), which suggested that the 1995-1996 year-class (=1996 year-class in the present study) was 'strong', whilst the 1994-1995 year-class (=1995 year-class in the present study) was 'weak'.

RELATIONSHIPS WITH FLOW

Year-class strength of barramundi was significantly and positively correlated with: annual flow (r=0.55); annual rain (r=0.67); summer flow (r=0.60; summer rain (0.50); spawning season flow (r=0.61); spawning season rain (r=0.63); and spring flow (r=0.66). YCS was not significantly correlated with freshwater flow or coastal rain in autumn or winter (Table 1). These results were consistent with those of Staunton-Smith et al. (2004). YCS of barramundi was significantly correlated with the annual stocking rate of barramundi fingerlings in the freshwater reaches of the Fitzroy River (r=0.37). This is in contrast to Staunton-Smith et al. (2004), who found no significant correlation between YCS and annual barramundi stocking.

All sub-sets general linear modelling identified several alternative models that explained ~85 to 90% of the variation in abundance of age-classes of barramundi (Table 2). The base model of age and sample year (i.e., forced variables) explained 62.0% of the variation in the abundance of age-classes. Inclusion of the additional terms summer freshwater flow, stocking rate and autumn rainfall (all positive) provided the 'best' model (overall adjusted R^2 = 90.4%) and was consistent with that of Staunton-Smith et al. (2004). The other 'best' model reported by Staunton-Smith et al. (2004; i.e., summer rain, spring flow and winter flow, overall adjusted R^2 = 85.9%), was not significantly better for the five years of data than the two term model of summer rain and spring flow (overall adjusted R^2 = 86.3%). This was a consequence of the winter flow term not significantly improving the two term model when five years of data were used. Other models with only two environmental terms also explained a high degree of the variation in age-class abundance, with all terms in the models positive in direction (Table 2). The models explained between 73.7% and 62.9% of the variation in abundance of barramundi age-classes not explained by age and sample year alone. Flow terms appeared in all four of these 'best' all sub-set models, whilst rainfall terms appeared in three of the four models. Interestingly, stocking of barramundi in the freshwater reaches of the Fitzroy River system influences YCS as well as the commercial catch of estuarine fish (Robins et al., 2005), although strong year-classes occurred even when stocking was low (e.g. 1991). These results indicate that mature stocked fish were moving from freshwater habitats (probably with freshwater flows i.e., floods) to estuarine waters to join the breeding population, as barramundi is catadromous. The impact of stocking on the abundance, genetic diversity and sustainability of the barramundi fishery with respect to the contribution of stocked versus wild recruits is poorly understood and requires further examination.

TABLE 2. Regression models explaining variance in the abundance of age-classes of barramundi sampled from the Fitzroy River estuary.

Regression model[A]	Percent variance accounted for (adjusted R^2)
Age, sample year	62.0
Age, sample year, summer flow, stocking, autumn rain	90.4
Age, sample year, summer flow, stocking	88.2
Age, sample year, spring flow, summer flow	86.3
Age, sample year, spring flow, summer rain	85.9

[A] Factors in the multiple regression were positively related to age-class unless otherwise indicated.
Age and sample year forced variables.

POSSIBLE CAUSAL MECHANISMS OF RELATIONSHIPS BETWEEN YCS AND FRESHWATER FLOW

Staunton-Smith et al. (2004) explored three possible causes as to why the year-class strength of barramundi would be related to freshwater flows into an estuary. They were: (i) increased egg production when land-locked fish are released by floodwaters and are then able to participate in spawning, as originally suggested by Dunstan (1959); (ii) increased survival during the first months of life when high coastal rainfall and freshwater flows generate access to supra-littoral nursery areas, improving the productivity and/or carrying capacity of the system; and (iii) enhanced survival of juvenile barramundi after leaving nursery habitats as a consequence of high river flows or flooding rain.

Results of the current 5-year study do not support the first possible causal mechanism as the majority of the fish leaving freshwater reaches are male (i.e., <800 mm and < five-years-old, Halliday unpublished data) and therefore do not increase the annual egg production of the region and summer flows releasing land-locked fish usually occur after the main spawning season has ended. The second possible causal mechansim is still valid, but otolith microchemistry indicates that barramundi do not use freshwater habitats until they are at least three-months-old (Milton et al., 2008). In addition, spring tides are probably more important in allowing juvenile barramundi (i.e., <50 mm) access to supra-littoral habitats (Russell & Garrett, 1985) than flooding flows. The third causal mechanism (i.e., enhanced survival of juveniles after leaving nursery habitats) is possible given that summer flows usually occur after the main spawning season has ended and these flows may well enhance the quality and availability of juvenile habitats in the estuary.

In addition to the mechanisms proposed by Staunton-Smith et al. (2004), it is likely that freshwater flows enhance the productivity of an estuary and support the food chains within them (Whitfield, 2005). It is possible that increased productivity associated with spring and summer flows to the estuary increase the number of juvenile barramundi surviving the first year of life (i.e., the 0+ age-class) via increased growth rates during this critical time. Robins et al. (2006) reported significant positive relationships between seasonal growth rates of juvenile (>170 mm TL) and adult barramundi, with freshwater flow, provided that flow was greater than 2 m^{3}sec^{-1}. Freshwater flow had the greatest effect on growth rates of barramundi in summer, where median or greater freshwater flows resulted in almost doubling the growth rates shown by barramundi during minimal flows (Robins et al. 2006). There is probably a delay between the occurrence of a freshwater flow and an increase in the productivity of an estuary in the order of weeks to months. Barramundi is an opportunistic carnivore. The trophic position of barramundi within the food chain increases as individuals grow in size (Bowles et al., 2001) and their diet changes from micro-crustaceans to macro-crustaceans to fish (Davis, 1987). The abundance of *Acetes* sp. and banana prawns (*Penaeus (Fenneropenaeus) merguiensis*), which are major prey items of young barramundi (Russell & Garrett, 1985; Robertson, 1988), are coincidentally and positively related to freshwater flow (Sumpton & Greenwood, 1990; Vance et al., 1998; Robins unpublished data). An increase in barramundi prey abundance with flow provides further evidence in support of a productivity mechanism, reliant on freshwater flows delivering nutrients (i.e., carbon and nitrogen) to the estuary, which improves the 'quality' and or 'quantity' of estuarine fishery habitats and the prey contained within them.

CONCLUSIONS

Our results support the persistence over time of the significant positive relationship between freshwater flow to the estuary and barramundi year-class strength. Barramundi are an iconic part of tropical Australian estuaries that support fishing industries. The consequences of changes in abundance and growth rates of estuarine barramundi populations should be explicitly considered by water managers when determining the ecological, economic and social costs of upstream water development and abstraction. Changes to freshwater flows as a consequence of long-term climate change may also impact upon the productivity of barramundi populations in Queensland.

ACKNOWLEDGEMENTS

The study was funded by the Cooperative Research Centre for Coastal Zone Estuary and Waterway Management, the Fisheries Research and Development Corporation and Agri-Science Queensland (a service of the Department of Employment, Economic Development and Innovation). We thank the seafood processors and commercial fishers of the Fitzroy River region for their cooperation and allowing access to the commercial catch of barramundi. Thanks also to Gary

Hargraves, Hans Mulder and Mike Keane (Department of Natural Resources, Mines and Energy, Queensland) and Quentin Rider (Fitzroy River Water) for providing freshwater flow data. We also thank two anonymous referees for their comments on the manuscript.

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