Chapter 6. Using age-structure of commercial catch to investigate the importance of freshwater flows in maintaining barramundi and king threadfin populations


Summary
The age-structures of the commercial catch of barramundi (*Lates calcarifer*) and king threadfin (*Polydactylus macrochir*) were examined over five consecutive years in a dry tropical estuary and used to estimate the year-class strength of each species. Variation in year-class strength was compared with variability in freshwater flowing to the estuary. The year-class strength of both barramundi (an opportunistically catadromous species) and king threadfin (a non-diadromous estuarine species) fluctuated and was significantly and positively correlated with freshwater flow and coastal rainfall in spring and summer. All sub-sets general linear models were used to screen potential relationships between year-class strength of each species and freshwater variables. Several alternate models were identified that explained ~85 to 90% of the variation in the abundance of age classes of barramundi and ~76 to 80% of the variation in the abundance of age classes of king threadfin.

The survival of young-of-the-year barramundi may be enhanced by freshwater flows by: (a) enhancing the access of larvae, post-larvae and juvenile barramundi to suitable nursery habitats in the estuary, such as temporary supra-littoral pools; (b) enabling a proportion of juvenile barramundi to access freshwater habitats intermittently linked to the estuary; and (c) increasing the productivity of the estuary (i.e. increased prey species abundance), with increased growth rates of post-larval and very young barramundi increasing the number of individuals that survive the first year of life.

We hypothesised that freshwater flows may influence the survival of larval and/or juvenile king threadfin in estuaries leading to increased year-class strength by: (a) enhancing the biological productivity of the estuary, thereby increasing prey species abundance resulting in improved growth rates of king threadfin; (b) affecting the area of favourable habitat through larger areas of decreased salinity, with lowered salinities affecting the energy budgets; and/or (c) creating turbid conditions reducing predation on juvenile king threadfin.

Freshwater flows in spring and summer are important drivers of the year-class strength of at least two important estuarine finfish species, and reduction in these flows, through the development of water infrastructure and abstraction or long-term climate change, will potentially reduce the size of the population of estuarine fish available for human harvest. In addition, these results suggest that stock assessments should consider the impacts of freshwater flows and or coastal rainfall on the annual recruitment of barramundi and king threadfin.

Introduction
The use of freshwater resources (e.g. for cities, industry and agriculture) has altered the magnitude, duration and timing of freshwater flowing into estuaries and impacted estuarine species (Drinkwater and Frank 1994; Gillanders and Kingsford 2002). Sustainable management of freshwater requires an understanding of the role (or importance) of freshwater flows in downstream biological processes, and how changing natural river flows impacts uponestuarine populations. A number of estuarine species are exploited by commercial, recreational or subsistence fisheries, and the management of these fisheries would also benefit from an

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understanding of factors other than fishing effort (i.e. environmental factors) that influence the population size (Shepard et al. 1984; Hilborn and Waters 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 freshwater flow and catch has been reported for numerous marine and estuarine species, often with time lags equaling 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 undertaken further investigation into 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.

Through conceptual models and review of life history’s (see Chapter 2), we identified that freshwater flows may affect the recruitment of estuarine fish species. There are a number of mechanisms by which enhanced recruitment may occur:

1) Transporting eggs and larvae away from the estuary (negative effect);
2) Creating chemical signals for larvae to enter the estuary and locate nursery habitats (positive effect);
3) Enabling post-larvae and small juveniles to move into supra-littoral nursery habitats; and
4) Enabling large juveniles to migrate into freshwater habitats intermittently linked to the estuary.

If freshwater flows do affect recruitment 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 and associated commercial catch. 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 the age-structure of adult populations of freshwater and marine species (e.g. Mills and Mann 1985; Maceina 1997; Morison et al. 1998; McGlenonn 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 a number of 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 this chapter was to determine whether there was evidence of variation in YCS in the adult population of long-lived estuarine fish species for which large scale variability in YCS has not yet been demonstrated, and if so, whether the variation could be related to freshwater flowing into the estuary. Life history review identified two estuarine fish species, barramundi (Lates calcarifer) and king threadfin (Polydactylus macrochir), whose YCS may be influenced by freshwater flow. 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 was sufficient to sample the adult populations adequately, thus negating the need to kill large numbers of fish during fishery-independent surveys.

The specific objectives of the study were to:

1) Estimate the age-structure of barramundi and king threadfin populations in the Fitzroy River region using samples from commercial catches;
2) Estimate YCS for barramundi and king threadfin populations;
3) Investigate whether variation in YCS of each species was related to patterns in the freshwater flowing into the estuary; and
4) Propose possible causal mechanisms for the observed relationships.
Methods

Sampling of commercial catch
Sampling of the commercial catch was scheduled to coincide with peaks in commercial fishing effort that occur in the weeks preceding and following the annual seasonal closure for barramundi (i.e. 1 November to 31 January). The commercial catch was sampled for five consecutive ‘sampling years’, with year-1 = 2000/01, year-2 = 2001/02, year-3 = 2002/03, year-4 = 2003/04 and year-5 = 2004/05. We sampled twice each ‘sampling year’, once in the week(s) preceding the seasonal fishing closure (i.e. October) and then again in the week(s) after the opening of the fishery (i.e. February). Sampling was concentrated at three seafood processors (two in Gladstone and one in Rockhampton, Figure 6.1), as these seafood wholesalers had previously been identified as consistently purchasing most of the estuarine fish caught by commercial fishers in the Fitzroy River region. Where possible, barramundi and king threadfin purchased by the processors during the sampling period were measured (total length (TL) for barramundi and caudal fork length (FL) for king threadfin) and otoliths were removed from as many of these fish as time permitted. We also identified approximately where each fish was caught, by questioning the processors or fishers. Sex of fish was not recorded, as the fish were ‘cleaned’ (i.e. gills and viscera removed) prior to arriving at the seafood processors.

Figure 6.1 Locality map of the Fitzroy River estuary (downstream of the city of Rockhampton) in central Queensland, Australia

Otoliths were blocked in resin, then sectioned at 300 μm. Sections were viewed using a microscope and reflected light. In general, there was very clear differentiation between the slow
(narrow, opaque, light) and fast (broad, translucent, dark) growth zones in barramundi otoliths from the Fitzroy River region (Stuart and McKillup 2002). Distinct increments probably occur because feeding and growth rates slow down greatly during the colder months in the Fitzroy River region, which is near the southern extremity of the distribution of barramundi and king threadfin in eastern Australia. Counts of the narrow, opaque increments were validated as having been laid down yearly and were counted to determine the fish age. However, an extra year was added to fish caught in October if an increment was not visible on the otolith’s edge (i.e. if they had a wide marginal increment). The justification for this procedure was that preliminary marginal increment analysis suggested increments are laid (or become visible increments around the margin) in or around October (see Appendix 6). Therefore, when an increment was not visible on the otolith’s edge in October, it was assumed that this was a visual artefact due to the curved nature of the otolith.

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 sampling trip (i.e. two trips per sampling year). A single age-structure was constructed for each sampling year. Year-classes were assigned on the basis of spawning year, when spawning occurs over spring and summer, with an assumed 1 January birthday (i.e. fish born in November 1990 and February 1991 are in the 1991 year-class).

Only barramundi from three- to eleven-years-old were included in the analysis as it was considered that these best represented the year-classes most effectively sampled by the net size restrictions in the commercial fishery (see Staunton-Smith et al. 2004; or Appendix 6 for details). For similar reasons, only king threadfin from two- to eleven-years-old were included in the analyses.

Estimating year-class strength
We used the method described by Maceina (1997) to estimate year-class strength (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.

Correlating year-class strength with environmental variables
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) all sub-sets general linear modelling (GenStat 2005) with year-class strength as the response, and age, sample year, freshwater flow variables and stocking as independent variables. Age was forced into the model, as was sampling year, because the abundance of individual age-classes is not comparable between years. Significant models with three additional independent terms were reported. We examined serial auto-correlation of regression residuals using residual maximum likelihood (REML, GenStat 2005), to investigate whether there was evidence that recruitment success was auto-correlated (e.g. due to stock-recruitment relationships). The results showed no significant auto-correlations, thus standard general linear modeling methods were used. The general linear models were used for data exploration and model screening. Ridge regression (GenStat 2005) 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 freshwater 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
coastal catchment of the estuary 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 and Water, 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). We also included a ‘spawning season’ aggregate of flow or rainfall, which is the sum of flow or rainfall during spring and summer i.e. September to February inclusive. 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. Analyses of king threadfin data did not include stocking, as this species is not stocked in the Fitzroy River. River flow, rainfall and stocking data were transformed (log$_{10}$+1) to normalise data and stabilise variances.

We made the following assumptions in our analysis:

1) Age-structure is determined mainly by recruitment;
2) Migration rates between estuaries were low;
3) Fish stocking does not bias the results; and
4) Age-structure of the adult population was estimated accurately.

The details and validity of these assumptions are discussed in Staunton-Smith *et al.* (2004), Halliday *et al.* (submitted) and Appendix 6.

**Results**

**Length-frequencies of samples**

A total of 2690 barramundi and 1185 king threadfin from the Fitzroy River region were measured during the five ‘sampling years’, with 2112 and 716 aged respectively (Table 6.1). There were consistent differences between the samples collected in October compared with those of the following February. Differences included the number of fish measured, as well as size-structure. The most notable difference was the large number barramundi <800 mm TL in February that were not present in the October samples (i.e. 78 and 69% of fish measured in February 2001 and 2002 c.f. 32 and 35% of fish measured in October 2000 and 2001).

<table>
<thead>
<tr>
<th>Sample year</th>
<th>Sample trip</th>
<th>Barramundi</th>
<th>King threadfin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year-1</td>
<td>October 2000</td>
<td>155</td>
<td>154</td>
</tr>
<tr>
<td></td>
<td>February 2001</td>
<td>495</td>
<td>413</td>
</tr>
<tr>
<td>Year-2</td>
<td>October 2001</td>
<td>155</td>
<td>128</td>
</tr>
<tr>
<td></td>
<td>February 2002</td>
<td>488</td>
<td>197</td>
</tr>
<tr>
<td>Year-3</td>
<td>October 2002</td>
<td>125</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td>February 2003</td>
<td>480</td>
<td>319</td>
</tr>
<tr>
<td>Year-4</td>
<td>October 2003</td>
<td>236</td>
<td>236</td>
</tr>
<tr>
<td></td>
<td>February 2004</td>
<td>240</td>
<td>237</td>
</tr>
<tr>
<td>Year-5</td>
<td>October 2004</td>
<td>72</td>
<td>69</td>
</tr>
<tr>
<td></td>
<td>February 2005</td>
<td>244</td>
<td>235</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2690</td>
<td>2112</td>
</tr>
</tbody>
</table>

The catch of barramundi ranged in age from two-years-old to 32-years-old (two individuals), with 8.3% of the sampled catch aged as two-years-old, 88.4% of the catch aged between three-
and eleven-years-old, 2.0% of the catch aged between 12- and 20-years-old and 1.3% of the sampled catch aged as greater than 20-years-old.

The catch of king threadfin ranged in age from one-year-old to 19-years-old (two individuals), with 3.1% of the sampled catch aged as one-year-old, 86.3% of the catch aged between two- and eleven-years-old, and 10.6% of the sampled catch aged between 12- and 19-years-old.

There was large variation in the length-at-age of both barramundi and king threadfin (Figure 6.2). For example, three-year-old barramundi may range in length range from 580 mm to 1000 mm TL. Three-year-old king threadfin may range in length from 500 mm to 850 mm FL. This shows that fish length is not a reliable indicator of fish age for barramundi or king threadfin. Similarly, a 1000 mm TL barramundi can be between three- and 13-years-old, whilst a 1000 mm FL king threadfin can be between four- and 16-years-old.

Figure 6.2 Length-at-age plots for a) barramundi and b) king threadfin sampled from the Fitzroy River estuary

Boxed area shows data used in the analyses of year-class strength (ages three- to 11-years-old for barramundi and two- to 11-years-old for king threadfin).

Age-structure
There was a systematic change in the age-structure of samples from year-1 to year-5 (Figure 6.3). In year-1, the five-year-old age-class was ‘strong’ for both species and could be followed in the yearly age structures over the five sample years. The two-year-old age-class for king threadfin was also strong and can be followed through the five sample years, becoming the six-year-old age-class in sample year-5 (Figure 6.3). For barramundi the six-, seven- and eight-year-old age-classes were ‘weak’ in year-1 and this pattern persisted throughout the sampling (Figure 6.3).
Using residuals from the catch-curve regression

The standardised residuals from the catch-curve regressions give an indication of relative year-class strength (YCS).

The 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 (Figure 6.4). 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. 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 (i.e. -0.5 to 0.0) and thus could not be classified as either ‘strong’ or ‘weak’ (Figure 6.4).


Figure 6.4 Residuals from catch-curve regressions of barramundi and king threadfin against summer freshwater flows from the Fitzroy River estuary

Correlating environmental variables with year-class strength

River flow and coastal rainfall were significantly correlated in spring, summer and autumn (r= 0.73, 0.78 and 0.63 respectively, P<0.05, n=14), but not in winter. They were also significantly correlated during the spawning season (i.e. September to February inclusive). These results suggest that seasonal river flow and coastal rainfall in summer, autumn and spawning season should have similar correlations with the measures of YCS. However, this was not always the case.

YCS of barramundi was significantly and positively correlated with freshwater flow and coastal rainfall annually, during summer and the spawning season (i.e. spring + summer), and was significantly and positively correlated with spring flow but not spring rain (Table 6.2). YCS was not significantly correlated with freshwater flow or coastal rain in autumn or winter. Stocking of
barramundi fingerlings in the freshwater reaches of the Fitzroy River was significantly correlated with YCS, although a strong year-class occurred when stocking was low (1991).

YCS of king threadfin was significantly and positively correlated with freshwater flow and coastal rainfall for annual totals, during spring and summer, as well as with the spawning season aggregate (Table 6.2). YCS of king threadfin was not significantly correlated with freshwater flow or coastal rainfall in autumn or winter. Correlation coefficients tended to be at least equal or of greater value for freshwater flow variables than for rainfall variables.

Table 6.2 Correlation coefficients (r) between estimated year-class strength (YCS) and freshwater flow and rainfall variables for barramundi and king threadfin in the Fitzroy River estuary

<table>
<thead>
<tr>
<th></th>
<th>Barramundi YCS</th>
<th>King threadfin YCS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual flow</td>
<td>0.55***</td>
<td>0.60***</td>
</tr>
<tr>
<td>Annual rain</td>
<td>0.67***</td>
<td>0.60***</td>
</tr>
<tr>
<td>Spawning season flow</td>
<td>0.61***</td>
<td>0.72***</td>
</tr>
<tr>
<td>Spawning season rain</td>
<td>0.63***</td>
<td>0.60***</td>
</tr>
<tr>
<td>Spring flow</td>
<td>0.66***</td>
<td>0.64***</td>
</tr>
<tr>
<td>Spring rain</td>
<td>0.17</td>
<td>0.44***</td>
</tr>
<tr>
<td>Summer flow</td>
<td>0.60***</td>
<td>0.61***</td>
</tr>
<tr>
<td>Summer rain</td>
<td>0.50**</td>
<td>0.32*</td>
</tr>
<tr>
<td>Autumn flow</td>
<td>0.16</td>
<td>0.21</td>
</tr>
<tr>
<td>Autumn rain</td>
<td>0.09</td>
<td>-0.06</td>
</tr>
<tr>
<td>Winter flow</td>
<td>-0.01</td>
<td>0.03</td>
</tr>
<tr>
<td>Winter rain</td>
<td>-0.24</td>
<td>-0.02</td>
</tr>
<tr>
<td>Stocking</td>
<td>0.37*</td>
<td>n/a</td>
</tr>
</tbody>
</table>

*= P<0.05, ** = P<0.01, *** = P<0.001; n/a = not applicable for king threadfin i.e. no stocking

All sub-sets general linear modelling identified several alternate models that explained ~85 to 90% of the variation in the abundance of age classes of barramundi and around 75% of the variation in the abundance of age classes of king threadfin (Table 6.3).

For barramundi, the base model of age and sample year (i.e. forced variables) explained 62.0% of the variation in the abundance of age classes. This is slightly greater that reported in Staunton-Smith et al. (2004) and is a consequence of an additional two years of data (i.e. sample year-4 and year-5). The additional terms of summer river flow, stocking and autumn rainfall (all positive) was the ‘best’ model (adjusted $R^2 = 90.4\%$) and is 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 consequence of the winter flow term not significantly improving the two term model. 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 being positive in direction (Table 6.3). 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. Spring and summer flow or rainfall was included in all ‘best’ models.

Interestingly, stocking of barramundi in the freshwater reaches of the Fitzroy River system influences YCS as well as the estuarine catch (Robins et al. 2005). Mature barramundi that were stocked as fingerling move from freshwater reaches with flows to estuarine waters (unpublished tag-recapture information, Australian National Sporting Association) and join the breeding population. The impact of stocked fish on the abundance, genetic diversity and sustainability of the commercial fishery with respect to stocked vs. wild recruits is poorly understood and requires further examination.
Table 6.3 Best all subset regression models for the abundance of age-classes of barramundi and king threadfin sampled from the Fitzroy River estuary

<table>
<thead>
<tr>
<th>Species</th>
<th>Regression model</th>
<th>Percent variance accounted for (adj. R²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barramundi</td>
<td>Age, sample year, summer flow, stocking, autumn rain</td>
<td>90.4</td>
</tr>
<tr>
<td></td>
<td>Age, sample year, summer flow, stocking</td>
<td>88.2</td>
</tr>
<tr>
<td></td>
<td>Age, sample year, spring flow, summer flow</td>
<td>86.3</td>
</tr>
<tr>
<td></td>
<td>Age, sample year, spring flow, summer rain</td>
<td>85.9</td>
</tr>
<tr>
<td>King threadfin</td>
<td>Age, sample year, summer flow, spring flow</td>
<td>76.4</td>
</tr>
<tr>
<td></td>
<td>Age, sample year, summer flow, spring rain</td>
<td>73.3</td>
</tr>
</tbody>
</table>

*Factors in the multiple regression are positively related to age class abundance unless otherwise indicated.

The base model of age and sample year (i.e. forced variables) explained 54.6% of the variation in abundance of year-classes of king threadfin. The best final two term model of summer flow and spring flow \((R^2 = 74.6\%)\) explained 44% of the residual variation from the base model. The only other significant two term model included summer flow and spring rain \((R^2 = 73.3\%)\) explained 42% of the residual variation from the base model. The relative influence of each term (summer flow and spring flow) on YCS was determined from the estimates in the ‘table of effects’ from the REML analysis (i.e. summer flow = 0.78, spring flow = 0.21; multiplied by the flow range). This indicated that summer flow as having an influence of approximately double that of spring flow on the strength of any given year-class of king threadfin. Significant positive serial autocorrelation of AR1 (i.e. a one year lag) was detected (REML, GenStat 2005) indicating that for king threadfin there was an increased likelihood of strong year-classes following strong year-classes and weak year-classes following weak year classes. Coefficients adjusted for AR1 were not significantly different than those derived from the standard GLM. Ridge regression correlations amongst the independent variables were not pronounced averaging 0.26 with a maximum of 0.36. These values indicated a low adjustment factor \((k\text{-coefficient})\) for the ridge regressions and in these ranges the ridge traces (i.e. the coefficient values for the independent variables) were stable. Therefore, the low degree of correlations amongst the independent variables was dismissed and standard general linear models adopted throughout. Significant correlation of the YCS of king threadfin and barramundi \((r = 0.57, P < 0.05)\) indicated that freshwater flows influenced the YCS of both species in a similar way.

Discussion

Using commercial catches to estimate the age-structure of the fish populations

Sampling commercial catches of barramundi and king threadfin via carefully selected seafood processors provided a reasonable estimate of the age-structure of the populations of these species in the Fitzroy River region. This approach was cost and time efficient, and allowed project staff to build a strong rapport with local seafood stakeholders (including commercial fishers). The value of this approach for the central Queensland region was recognised by the Long Term Monitoring Program of the DPI&F, who have adopted a sampling program for barramundi based on this approach (i.e. via seafood processors), the information from which is used in the ongoing stock assessment of barramundi.

Estimating year-class strength

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 the recruitment of barramundi and king threadfin in the Fitzroy River region. The success of the method, i.e. using otoliths to estimate age-structure and hindcast year-class strength is dependent on being able to: (i) representatively sample the population; and (ii) confidently estimate the absolute age of individual fish (compared to estimating relative age) so that a birth-year can be assigned; and (iii) repeatedly sample the population for a number of years, with three years being the minimum.
The ability to sample a species adequately is a potential problem when estimating relative rates of annual recruitment, especially if measuring the abundance of a single life history stage. The distribution of small and juvenile barramundi and king threadfin is not known in the Fitzroy River region, and as such would be difficult to sample representatively. In contrast, sampling the adult life history stage of barramundi and king threadfin in the estuary (e.g. from the commercial catch) represents a convenient method for comparing the relative abundance of numerous year-classes (see Staunton-Smith et al. 2004).

Otoliths from barramundi and king threadfin sampled from the Fitzroy River estuary had clearly defined opaque and translucent bands (Figure 6.5). In addition, ages of known-age barramundi were estimated from otoliths and used to validate our ability to estimate absolute age (see Staunton-Smith et al. 2004). Not only are increments laid annually, but the first increment was also identified accurately, which is often a problem (Morison et al. 1998).

Possible causal mechanisms of relationships between YCS and freshwater

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 barramundi and king threadfin populations over five consecutive years, suggests that recruitment variability has the potential to influence adult stock size in at least these species.

Variation in year-class strength (YCS), as an indicator of the overall recruitment and survival of juvenile barramundi and king threadfin, was consistently and positively related to the amount of freshwater flowing into the Fitzroy River estuary during spring or summer. We would not expect barramundi and king threadfin to show the same patterns in the strength of recruitment (i.e. year-class strength), as barramundi are more tolerant of (and use) freshwater (habitats) whilst king
threadfin do not tolerate (or use) 0 salinity water (or habitats). However, we would expect some overlap in years of strong (or weak) recruitment as both species are carnivorous and would probably exploit any trophic blooms occurring in the estuary proper. Thus, although there may be some overlap in the causal mechanisms between year-class strength and freshwater flow for barramundi and king threadfin, we will consider each species separately.

Barramundi – a diadromous species

The significant correlations 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 estuaries during spring and summer (Dunstan 1959; Russell and Garrett 1983, 1985; Davis 1985). Life history assessment identified four causal mechanisms by which the recruitment (=YCS) of barramundi could be related to freshwater flow (see Chapter 2). These were:

1) transporting eggs and larvae away from the estuary (negative effect);
2) creating chemical signals for larvae to enter the estuary and locate nursery habitats (positive effect);
3) enabling post-larvae and small juveniles to move into supra-littoral nursery habitats, and
4) enabling large juveniles to migrate into freshwater habitats intermittently linked to the estuary.

Life history assessment also identified a casual mechanism affecting the productivity of the estuary, which through increased food availability, could improve the growth and survival of post-larvae, juveniles, adolescents and adults.

The above mechanisms are not mutually exclusive, and it is unlikely that they represent the only mechanisms by which freshwater flows affect the survival of juvenile barramundi. For example, YCS may be related to the size of the spawning population. This causal mechanism is based on increased egg-production and subsequent numbers of juvenile fish in years when floodwaters release land-locked fish, as proposed by Dunstan (1959). However, most fish migrating from freshwater habitats are likely to be males and it is uncertain whether enough mature females arrive from freshwater habitats to increase egg production greatly.

Our results provide no evidence that freshwater flows transport the eggs and larvae of barramundi away from the estuary (i.e. mechanism (a) above). The remaining causal mechanisms relate to access or attraction to estuarine nursery habitats (i.e. mechanisms (b) and (c) above), access to freshwater habitats (i.e. mechanism (d) above) and enhanced productivity (i.e. a trophic response) within the estuary. As the method reported herein is correlative, the following discussion is speculative and requires further investigation.

Freshwater flows may enhance the survival of barramundi during their first months of life, by enhancing the access of larvae, post-larvae and juveniles to suitable nursery habitats. The larvae and very young juveniles of barramundi have been observed in ephemeral supra-littoral nursery habitats in close proximity to spawning areas, such as coastal swamps and lagoons and supra-littoral pools on salt pans (Dunstan 1959; Moore 1982; Russell and Garrett 1983, 1985; Davis 1985; Griffin 1987). The spatial and temporal extent of many of these nursery habitats is affected by the amount of freshwater runoff, and access to and from them is dependent on seasonally high 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 unknown. However, they could include the substantial supra-littoral 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 supra-littoral nursery areas, extending the spatial or temporal extent of ephemeral nursery areas, increasing their productivity and carrying capacity (i.e. abundance of
prey species), and or increasing their suitability in some other way (e.g. physico-chemical characteristics). However, otolith microchemistry indicates that barramundi are not using freshwater habitats until they are at least three-months-old (see Chapter 8; Milton et al. submitted) and spring tides are probably more important in allowing juvenile barramundi (i.e. <50 mm TL) access to important supra-littoral nursery habitats (Russell and Garrett 1985).

Freshwater flows may enhance the survival of juvenile barramundi and the subsequent size of the adult population by enabling a proportion of juvenile barramundi to access freshwater habitats intermittently linked to the estuary. Migration of juvenile barramundi into upstream habitats typically occurs at the end of the wet season (Russell and Garrett 1983, 1985). However, only a proportion of juvenile barramundi migrate upstream as individual barramundi can complete their entire life-cycle in estuaries and coastal waters (Griffin 1987; Russell 1990). In the Fitzroy River, juvenile barramundi, mainly between 250 and 400 mm TL and about one-year-old, migrate 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. Our results do not provide evidence either for or against this mechanism.

Current results do not support the theory that freshwater flows allow access to wetland areas for juvenile barramundi. Instead large king tides are the probably the drivers of juvenile habitat access especially when barramundi are very small (i.e. <50 mm TL). Movement into and out of supra-littoral habitats on each tide has been reported (Russell 1987).

Freshwater flows may enhance the productivity of the estuary, with increased growth rates of post-larval and juvenile barramundi increasing the number of individuals that survive the first year of life. If this occurs, then our results suggest that it is productivity resulting from spring and summer freshwater flows that is important in driving the growth and survival of young-of-the-year barramundi. In Chapter 7, we report on the analysis of tag-recapture data that shows significant positive correlations between growth rates of juvenile and adolescent barramundi and the size and timing of freshwater flows. If the results from Chapter 7 hold true for post-larval and young-of-the-year barramundi, then it is highly likely that year-class strength of barramundi is being driven by the effects of freshwater flow on trophic productivity. There is probably a time lag between the occurrence of a freshwater flow and a bloom in trophic productivity of the estuary, especially at the trophic level of barramundi, which even as a juvenile is a higher order carnivore.

Barramundi has an ontogenetic change in diet, from micro-crustaceans to macro-crustaceans to fish (Davis 1987). The abundance and biomass of Acestes and banana prawns, which are likely to be major prey items of young-of-the-year barramundi, are coincidental and positively related to freshwater flow (see Chapters 9 and 10). This provides further evidence in support of a productivity mechanism, where a trophic cascade (or bloom) occurs as a result of freshwater flows delivering nutrients to the estuary and improving the ‘quality’ and or ‘quantity’ of nursery habitats of estuarine fishery species.

**King threadfin**

Variation in year-class strength (YCS), as an indicator of the overall recruitment and survival of juvenile king threadfin, was consistently and positively related to the amount of freshwater flowing or coastal rainfall delivered into the Fitzroy River estuary during spring and summer. These results are the first to provide quantitative evidence in support of increased survival of juvenile king threadfin with increased wet season freshwater flow (or rainfall).

Significantly less detailed information is available about the life history of king threadfin in northern Australia than for barramundi. King threadfin does not access freshwater habitats and will avoid waters of 0 salinity, but may utilise the salinity gradient in estuaries created by freshwater flows. We identified six possible ways in which freshwater flow may affect king
threadfin (see Chapter 2). From the limited quantitative information available on the life history of king threadfin, we hypothesised that freshwater flows may influence the survival of larval and/or juvenile king threadfin in estuarine habitats leading to increased year-class strength by:

1) enhancing the biological productivity of the estuary, thereby increasing the availability of food resulting in improved growth; (Whitfield 2005; Robins et al. 2006) and/or

2) affecting the area of favourable habitat potentially through larger areas of decreased salinity, with lowered salinities affecting the energy budgets (Cardona 2000); and/or

3) creating turbid conditions reducing predation, enhancing survival rates (Hecht and van der Lingen 1992).

While none of these hypotheses have been directly addressed for king threadfin, the significant positive correlations between spring and summer freshwater flow and YCS provides evidence for the hypothesis that freshwater flows positively influence the survival of larval and juvenile king threadfin which are reflected in the age structure of the commercial fishery years later.

Commonalities between species

The YCS of barramundi and king threadfin have a similar positive response to summer flows, despite different tolerances by juveniles of each species for lower salinity water that occurs as a consequence of freshwater flows.

The significant correlation between the YCS of barramundi and king threadfin suggest that young-of-the-year of both species have similar levels of survival in response high and low spring and summer freshwater flows. Recruitment patterns for both species were similar in 1996 and 1999 (i.e. strong) and 1993, 1994, 1995, 1997 and 1998 (i.e. weak). In 1992, the estimate of YCS differs, with king threadfin having a weak YCS and barramundi having a strong YCS. Coastal rainfall was above average in 1992, and was the only year when there was high coastal rainfall but low freshwater flow into the Fitzroy River estuary. The high coastal rainfall may have allowed young-of-the-year barramundi to exploit low salinity habitats adjacent or connected to the main estuary that are not available to young-of-the-year king threadfin because of salinity preference limitations.

Overlap in recruitment variation would be expected as both species are carnivorous and would probably exploit any trophic blooms occurring in the estuary as a consequence of flow events. In addition, both species have a spawning season that extends over several months, thus allowing early life-history stages to exploit the benefits of freshwater flows that vary in timing from year to year in northern Australia.

The current paradigm suggests that juvenile barramundi access supra-littoral and freshwater wetlands where ever possible, whilst juvenile king threadfin occur in the estuary before freshwater flows, leave once the freshwater flow has lowered the salinity, and return on the intruding salinity wedge. Banana prawns are a major component in the diet of both these species of fish, and variability in banana prawn abundance within the estuary may significantly affect the availability of prey for young-of-the-year barramundi and king threadfin. The abundance of juvenile banana prawns varies seasonally, generally peaking in autumn and probably being related to the volume and timing of freshwater flows (see Chapter 9), and may be a function of increased growth rates of juvenile banana prawns (see Chapter 9). Acestes is another macro-crustacean whose populations are highly responsive to freshwater flow (see Chapter 10) and who are a major prey item for barramundi and king threadfin.

Implications for fisheries production (e.g. commercial catch)

Fisheries catch (commercial and recreational) is affected by the cumulative history of everything that has happened to all year-classes of the fished stock plus factors that effect fisheries, such as gear selectivity, effort, and management restrictions. The results of the present chapter (i.e.
variation in YCS related to freshwater flow) have implications for the fisheries management of barramundi and king threadfin. In particular, these results suggest that stock assessments should consider the impacts of freshwater flows and or coastal rainfall on the annual recruitment of barramundi and king threadfin. Furthermore, because freshwater flows affect recruitment on a catchment basis, it is likely that stock assessments should be conducted regionally rather than at large spatial scales, such as the whole of the Queensland east coast. This is particularly relevant when a significant proportion of regional populations do not undertake long-shore migration.

**Implications for water management**

For at least two of the main estuarine commercial fisheries species in tropical Australia, spring and summer flows are important in determining the size of year-classes of fish, which subsequently mature and enter the fishery. Whilst current water infrastructure is unable to impede the flow of very large floods, it is important that managers (and politicians and the general public) are made aware that freshwater flowing to estuaries is not wasted, but rather supports the maintenance of estuarine fish populations.

Further research and numerical modelling is required before a robust estimate can be made of the extent to which the quantity, duration or frequency (e.g. number per decade) of freshwater flows could be modified and what effects these modified flows would subsequently have on estuarine fish populations. The aim of such work would be to achieve water efficiencies in environmental flow allocations i.e. how to achieve the same effect with less water. While the underlying mechanisms for strong YCS in years of high spring and summer flows are yet to be determined it appears likely that if freshwater flows to the estuary are reduced in spring and summer there will be a reduction in the abundance of these fish species.
Chapter 7. Effects of freshwater flow on growth rates of estuarine fish

J. Robins, D. Mayer, I. Halliday and J. Staunton-Smith

Summary
Relationships between freshwater flows and growth rates of an opportunistic predatory finfish (barramundi, *Lates calcarifer*) in a dry tropical estuary were examined using data from a long-term tag-recapture program. Lagged effects were not investigated.

After accounting for length-at-release, time-at-liberty and seasonal variation (e.g., winter, spring, summer, autumn), growth rates were significantly and positively related to freshwater flowing to the estuary. Effects were present at relatively low levels of freshwater flow (i.e. 2.15 m$^3$s$^{-1}$, the 5th percentile of the mean flow rate experienced by fish in the study during time-at-liberty).

The analysis, although correlative, provides quantitative evidence to support the hypothesis that freshwater flows are important in driving the productivity of estuaries and can improve growth rates of species high in the trophic chain.

Introduction
One of the hypotheses about freshwater flows to estuaries is that they stimulate the productivity of the estuary. In general, this refers to the nutrients being brought to the estuary that stimulate a bloom in primary productivity (i.e. phytoplankton) and have flow-on effects for higher levels in the trophic chain. Fish may benefit from the increase in productivity because of greater availability of food. An increased abundance of food (and its subsequent consumption) has been suggested to result in faster growth rates of finfish and shellfish (Aleem 1972; Turek *et al.* 1987; Drinkwater and Frank 1994; Quiñones and Montes 2001; Salen-Picard *et al.* 2002; see also Chapter 5). Although widely speculated upon, few studies have quantified the relationship between freshwater flow and growth rates of estuary finfish (but see De Graaf 2003).

Sawynok (1998) investigated the relationship between freshwater flow and growth rates of barramundi in central Queensland. Sawynok (1998) suggested that the average linear daily growth of barramundi in the Fitzroy River system was lower for flows less than 2.5 million Ml year$^{-1}$ than for flows greater than 2.5 million Ml year$^{-1}$ (i.e. 0.61 mm/day/fish compared to 0.90 mm/day/fish). Average linear daily growth of barramundi was based on 181 individuals tagged and recaptured within the same ‘tagging’ year, which had an initial total length of between 300 and 450 mm, were at liberty for >30 days and whose growth was positive.

Freshwater flow is only one of many environmental factors likely to influence the growth rates of fish within and between years. Season, particularly related to temperature, is a well-documented environmental effect on the growth rates of finfish. For barramundi, growth is strongly seasonal (i.e. like a cosine wave) with rates increasing from mid-spring (October) to the start of autumn (March) and decreasing from autumn to mid-spring (Dunstan 1959; Davis and Kirkwood 1984; Xiao 1999, 2000). Seasonal growth is also evident in sectioned otoliths of barramundi, where annular ‘bands’ are present in the otoliths, with the opaque zone representing slow growth being laid down before October (see Chapter 6; Staunton-Smith *et al.* 2004), and coincides when water temperatures are lowest. Xiao (1999) suggested that strong seasonal growth was potentially related to seasonal availability of food and seasonal changes in water temperature.

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Our aim in the present chapter was to re-assess the length differences in ANSA tagged-recaptured barramundi, include additional recapture data, and after accounting for seasonal growth, quantify the relationships between growth and freshwater flow conditions.

**Methods**

**Tagged fish data**

Tag-recapture data were obtained from the Suntag Program of the Australian National Sport Fishing Association Queensland Inc. (ANSA Qld). This catch and release tagging program aims to generate data for resource management purposes and has been ongoing in the Fitzroy River catchment and adjacent areas since 1984. A variety of freshwater, estuarine and marine species are caught, tagged and released by mostly recreational anglers. Recapture of tagged fish may be by ANSA Qld members, other recreational anglers, commercial fishers or researchers. Capture methods include limited cast-netting, line fishing with lures and bait (i.e. by recreational fishers) and gill-netting with mesh sizes ranging between 135 mm to 180 mm (i.e. by commercial fishers).

At the time of accessing, the Suntag database included 58 000 records of tagged fish of 154 ‘species’ tagged and recaptured between October 1984 and November 2004. Information available from tag and recapture events included tag number, date, total length in mm (TL), location of capture, and fisher. From this information, time-at-liberty, length-at-release, length-at-recapture, release year, release month, recapture year, recapture month, release location type, and recapture location type were calculated. From the available data, records that met the following criteria were selected: (i) species = barramundi; (ii) region of release and recapture = Fitzroy River catchment; (iii) time-at-liberty (in days) >30 and <366; and (iv) change in total length >0 mm. Selection of fish with a least 30 days between release (i.e. tagging) and recapture negated the need to consider tagging effects on growth rates (Reynolds and Moore 1982; Wang and Jackson 2000). Release and recapture locations were classified to account for the possibility that habitat type influences growth rates, as suggested by Davis and Kirkwood (1984). Anecdotal reports indicate juvenile barramundi grow faster in aquatic habitats with salinities less than that of seawater, suggesting that the habitat type in which a barramundi is tagged and recaptured should be considered as a cofactor during growth analyses. Release and recapture locations were classified into three types: (i) estuarine creek; (ii) estuarine river; and (iii) flood plain lagoon, which are freshwater areas intermittently connected to the estuary by floods. Movement of individuals between habitat types was examined. The majority of movement (~50%) involved individuals released in estuarine river habitats moving to estuarine creek habitats, but remaining within the estuary of the Fitzroy River.

**Freshwater flow data**

Freshwater flow data were obtained from the Department of Natural Resources and Water. The freshwater flowing to the estuary (end-of-system, EOS) was estimated as being gauged stream flow at the most downstream gauging station (i.e. at ‘The Gap’, 142.1 km Adopted Middle Thread Distance, ~23°5’S, 150°6’E ), minus the estimated seasonal extractive uses provided by the Department of Natural Resources and Water and Fitzroy River Water. Flow-during-liberty was calculated as the sum of estimated EOS flows of the Fitzroy River for the period during which individual tagged barramundi were at liberty i.e. flow-during-liberty is specific for each tagged individual.

**Analysis**

The data were explored using graphical methods and general linear models. Data patterns were noted, and three outliers identified and excluded from subsequent analyses.

The non-linear von Bertalanffy equation (Ratkowsky 1986) remains the cornerstone for analyses of finfish growth data, primarily because it has a single parameter (K) representing growth rate. In
alternate equations, such as the Schnute model (Ratkowsky 1986) or the function of Xiao (2000), growth rate is incorporated into two or three parameters, with a diminished capacity to incorporate environmental effects. Problems with the von Bertalanffy equation include a postulated relationship between the variance of the residuals and the fitted values (Sainsbury 1980), but this did not occur with our data. Also, the estimates of $K$ (the growth rate) and $L_\infty$ (the population’s average asymptotic length) can be correlated, but this is more of a problem when comparing analyses between different data sets. The current analysis fits a single data set.

Seasonality of growth is a known and major effect with barramundi (Xiao 2000), so the seasonal form of the von Bertalanffy equation (Somers 1988) was adopted as the starting model using GenStat (2005). This form is

$$L_t = L_{t-\delta} + (L_\infty - L_{t-\delta})(1 - e^{-K\delta_t}S(t-\delta_t))$$

where $L_t$ is the length-at-recapture, $t$ is the day of recapture, $\delta$ is time-at-liberty (days), $L_{t-\delta}$ is length-at-release, $L_\infty$ is the asymptotic length, $K$ is the average exponential growth rate, and

$$S(i) = \frac{C \sin[2\pi(i - t_s)]}{2\pi}$$

where $C$ measures the magnitude of the seasonal oscillation and $t_s$ is the time shift for the annual cycle (Somers 1988).

Parameters to be estimated are $L_\infty$, $K$, $C$, and $t_s$. This equation directly incorporates the effects of time-at-liberty, seasonality, and length-at-release. The effects of freshwater flows on growth rates were incorporated into the growth coefficient, $K$, as described below. A log-linear relationship of flow was superior to linear, and a threshold value (below which flow had no effect) was also found to be significant ($P<0.05$). Thus, in the equation above, $K$ was expanded to be $K_s + (K_s \{\text{flow - threshold}\} \{\text{if flow > threshold}\})$. Other factors were screened for their effects on growth using general linear models. Recapture-year was significant, but year was correlated with freshwater flow, so the latter was inferred as the more likely cause of growth differences. Release and recapture habitat type (i.e. estuarine creek, estuarine river, and flood plain lagoon) were not significant ($P>0.05$) and so were not included in the final model. The final model had an adjusted $R^2$ of 91%.

Assumptions and limitations

We assumed that: (i) lag effects between flow and growth rates were not significant; and (ii) the effects of measurement errors on growth rates were insignificant. The details and validity of these assumptions is discussed further in Robins et al. (2006), see Appendix for Chapter 7.

Results

A total of 1168 tagged and recaptured barramundi satisfied the selection criteria and were used in the analysis. Length-at-release ranged from 170 to 910 mm TL (Figure 7.1), although ~90% of fish were <600 mm TL and were probably juveniles or young adults. Barramundi were tagged throughout the year, with ~85% tagged between spring (September) and mid-autumn (April). The data were distributed within and across seasons, with 346 fish at-liberty during one season, 273 fish at-liberty over two seasons, 273 fish at-liberty over three seasons and 276 fish at-liberty over four seasons (Table 7.1). Mean daily growth rates (i.e. change in TL/days-at-liberty) varied between individuals of the same length-at-release (Figure 7.2). The greatest change in length (i.e. 380 mm by a 200 mm TL length-at-release individual at-liberty for 352 days) is similar to the greatest change in length within one year reported for barramundi tagged and recaptured by researchers in Papua New Guinea (Reynolds and Moore 1982).

There was considerable variety in the range of freshwater flow during-liberty experienced by barramundi included in the current study (Figure 7.3), including a 1-in-100 year flood. In terms
of release-location-type, 93% of barramundi were released in estuarine river habitats, and 4% and 3% were release in flood plain lagoon and estuarine creek habitats respectively. About 46% and 52% of barramundi were recaptured in estuarine river and estuarine creek habitats, respectively, with only 2% being recaptured in flood plain lagoons.

**Figure 7.1 Size of barramundi tagged, released and recaptured within the Fitzroy River estuary (n=1168)**

![Size of barramundi tagged, released and recaptured within the Fitzroy River estuary (n=1168)](image)

**Figure 7.2 Growth rates (mm/day) of barramundi tagged, released and recaptured within the Fitzroy River estuary (n=1168)**

![Growth rates (mm/day) of barramundi tagged, released and recaptured within the Fitzroy River estuary (n=1168)](image)

**Table 7.1 Duration and seasonal distribution of time-at-liberty of barramundi tagged, released and recaptured in the Fitzroy River estuary (n=number of fish)**

<table>
<thead>
<tr>
<th></th>
<th>One season</th>
<th>Two seasons</th>
<th>Three seasons</th>
<th>Four seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>spring</td>
<td>35</td>
<td>spring summer 95</td>
<td>spring summer autumn 34</td>
<td>spring summer autumn winter 25</td>
</tr>
<tr>
<td>summer</td>
<td>200</td>
<td>summer autumn 110</td>
<td>summer autumn winter 78</td>
<td>summer autumn winter spring 119</td>
</tr>
<tr>
<td>autumn</td>
<td>103</td>
<td>autumn winter 36</td>
<td>autumn winter spring 70</td>
<td>autumn winter spring summer 131</td>
</tr>
<tr>
<td>winter</td>
<td>8</td>
<td>winter spring 32</td>
<td>winter spring summer 91</td>
<td>winter spring summer autumn 1</td>
</tr>
<tr>
<td>Total</td>
<td>346</td>
<td>273</td>
<td>273</td>
<td>276</td>
</tr>
</tbody>
</table>
Figure 7.3 Freshwater flow (ML) experienced by barramundi tagged, released and recaptured within the Fitzroy River estuary during their time-at-liberty (days), y-axis presented on a log$_{10}$ scale, (n=1168)

Relationships between growth and freshwater flow

The estimated biological parameters (i.e. $L_\infty = 1829$ mm, $C = 1.045$ and $t = 19.4$) and average growth rates of different sized fish (Table 7.2) were all in agreement with other sources (e.g. Reynolds and Moore 1982; Griffin 1988; Fishbase 2004). As expected, growth rates of barramundi in the Fitzroy River estuary were strongly seasonal, and were fastest in summer and slowest in winter. Freshwater flow had a major interaction with season (Figure 7.4), having minimal effect on growth rates in winter and greatest effect on growth rates in summer (i.e. compared to average seasonal $K$, Table 7.2).

Table 7.2 Growth parameters for barramundi in the Fitzroy River estuary estimated under varying length-at-release and freshwater flow conditions

<table>
<thead>
<tr>
<th>Length-at-release (TL in mm)</th>
<th>Freshwater flow (m$^3$sec$^{-1}$)</th>
<th>Annual $K$ (yr$^{-1}$)</th>
<th>Average Seasonal $K$</th>
</tr>
</thead>
<tbody>
<tr>
<td>420$^a$</td>
<td>2.15$^a$</td>
<td>0.238</td>
<td>0.461 0.255 0.015 0.223</td>
</tr>
<tr>
<td>420$^b$</td>
<td>54.5$^a$</td>
<td>0.418</td>
<td>0.810 0.448 0.026 0.393</td>
</tr>
<tr>
<td>420$^c$</td>
<td>730.6$^a$</td>
<td>0.562</td>
<td>1.089 0.603 0.035 0.528</td>
</tr>
<tr>
<td>220$^a$</td>
<td>54.5$^a$</td>
<td>0.478</td>
<td>0.925 0.512 0.030 0.448</td>
</tr>
<tr>
<td>640$^b$</td>
<td>54.5$^a$</td>
<td>0.353</td>
<td>0.683 0.378 0.022 0.331</td>
</tr>
</tbody>
</table>

$^a$ = 50th percentile (median), $^b$ = 5$^{th}$ percentile, $^c$ = 95$^{th}$ percentile, $^e$ = break-point (critical threshold)

During summer, median or greater freshwater flows resulted in about twice the growth rates of minimal flows. For example, at the peak of the seasonal growth curve, growth for a 420 mm TL barramundi is 0.81 mm/day compared to 0.46 mm/day for flows of ~55 m$^3$sec$^{-1}$ and ~2 m$^3$sec$^{-1}$ respectively. The threshold at which freshwater flows affected seasonal growth (i.e. below which freshwater flow had no effect) was ~2 m$^3$sec$^{-1}$, which is equivalent to the 5$^{th}$ percentile of the freshwater flow during-liberty experienced by fish in the current study (Figure 7.5).
Figure 7.4 Seasonally adjusted growth curves for barramundi in the Fitzroy River estuary under various freshwater flow conditions*, modelled for: (a) 220 mm; (b) 420 mm and (c) 640 mm (total length) fish, which are the $5^{th}$, $50^{th}$ and $95^{th}$ percentiles of the sizes of barramundi tagged, released and recaptured.

* - 2 m$^3$sec$^{-1}$, 55 m$^3$sec$^{-1}$ and 730 m$^3$sec$^{-1}$ are the $5^{th}$, $50^{th}$ and $95^{th}$ percentiles of flow-during-liberty experienced by barramundi tagged, released and recaptured in the Fitzroy River estuary between 1984 and 2004.
Discussion

The analysis of tag-recapture data for barramundi in the Fitzroy River estuary, collected over almost 20 years, clearly demonstrates that: (a) growth rates vary seasonally; and (b) variable growth of barramundi is significantly related to the freshwater flows experienced by individuals, although other factors (e.g. genetic variation) are also likely to be important. The analyses do not account for lag effects between freshwater flows and growth, although such effects may exist.

In the current study, the threshold at which freshwater flows affected seasonal growth (i.e. 2 m$^3$ sec$^{-1}$) was an order-of-magnitude lower than the threshold identified by Sawynok (1998) of 79.3 m$^3$ sec$^{-1}$ (= 2.5 million Ml year$^{-1}$), who undertook more simplistic and less quantitative analyses using annual flow. This result may reflect the greater complexity of the current analysis, with the inclusion of seasonality allowing greater resolution of the effects of freshwater flow. The value identified by Sawynok (1998) is similar to the median annual flow in the Fitzroy River, above and below which seasonal growth rates (particular summer growth) are faster or slower respectively.

Variation in growth with freshwater flow might explain the inability of Davis (1987) to determine a reliable overall growth curve for barramundi from six rivers in northern Australia. He suggested that variability in growth was a reflection of different environmental conditions. We suggest that freshwater flow is probably a major factor of the environmental condition that Davis (1987) postulated to influence growth. Davis (1987) goes onto say that “these vast aquatic habitats formed during the summer monsoons provide juvenile barramundi with an almost predator-free prey-rich environment promoting rapid growth and improved survival”. The probability of highly variable growth resulting from adaptive phenotypic plasticity, dependent on the conditions to which an individual is exposed was also suggested by Morita and Morita (2002). This probably applies to barramundi, which is a euryhaline, opportunistic predator, with a non-obligatory catadromous life-cycle.

Numerous aspects of the barramundi life-cycle are likely to have evolved to take advantage of the flood-drought conditions of northern Australia, with growth being one example. Recruitment of barramundi has been quantitatively related to freshwater flow (Staunton-Smith et al. 2004; see Chapter 3 and 4), as has its catchability (Robins et al. 2005; see Chapter 3 and 4). Indeed, faster growth (as a consequence of higher freshwater flows) may lead to increased survival of young-of-the-year barramundi (i.e. < ~450 mm TL) which would enhance the strength of the year-class.

Figure 7.5 Thresholds of the effect of freshwater flow-during-liberty on seasonal growth rates of barramundi within the Fitzroy River estuary, x-axis presented on a log10 scale.
during higher flow conditions. As such, the results of the current chapter are consistent with those of Chapter 6 (published as Staunton-Smith et al. 2004), where significant correlations were found between age-based assessments of year-class strength of barramundi and freshwater flow into the Fitzroy River estuary.

Possible causal mechanisms of relationships between fish growth and freshwater flow

Commercial and recreational fishers anecdotally report that barramundi grow faster in freshwater habitats than saltwater habitats, and Dunstan (1959) commented that for fish of the same length, barramundi from freshwater habitats are heavier than those from saltwater. However, in the current analysis, the inclusion of release and recapture location type (i.e. estuarine creek; estuarine river; and flood plain lagoon) did not significantly improve the model. It may also be that more fish from different habitats, especially flood plain lagoons are needed to detect habitat effects or we may need to assess weight rather than length data.

Freshwater flows are speculated to affect the growth rates of estuary-associated fish such as barramundi by a number of mechanisms. Freshwater flows to estuaries lower salinities for varying periods, with the lowered salinity then affecting the energy budgets of estuarine fish species. For example, Cardona (2000) examined the effects of salinity on the habitat selection and growth of mullet (Mugil cephalus Linnaeus), which is a euryhaline and non-obligatory catadromous species. Cardona (2000) speculated that the growth of euryhaline species was affected by salinity because the energy used for osmo-regulation is not available for growth. Results in the present study of higher growth rates at higher freshwater flows (= lowered salinities in the estuary), and the anecdotal reports of higher growth in freshwater habitats, would be consistent with this hypothesis.

Trophic linkages are another mechanism by which freshwater flows (i.e. floods) may influence the growth rates of finfish. This is a common speculation (Aleem 1972; Turek et al. 1987; Drinkwater and Frank 1994; Quiñones and Montes 2001; Salen-Picard et al. 2002; see also Chapter 5), with the theory that the abundance and or accessibility of prey affect the growth rates of predators (Zimmerman et al. 1990). Darnaude et al. (2004) linked the flood-related pulses in short and long-lived polychaete species to increased growth and survival of sole (Solea solea Linnaeus) using stable isotope analysis, supporting previously reported relationships between river runoff and the coastal fishery production of sole in the Gulf of Lions (Salen-Picard et al. 2002). The result of Darnaude et al. (2004) provides quantitative evidence of the existence of trophic links between freshwater flow and fisheries production through enhanced growth and survival. Barramundi is an opportunistic ambush predator that is likely to exploit any pulses in prey availability related to trophic responses to flood events, in either estuarine or freshwater habitats. Further research would be needed to determine if relationships between freshwater flow and growth rates are common phenomena for other estuarine-dependent finfish species. Platten (2005; see chapter 5) presents further evidence in support of trophic linkages resulting in increased growth rates of estuarine-associated finfish.

Implications for water management

Climatic variation in the strength of the wet season in northern Australia is the primary driver of variation in freshwater flow, although the development of water resources in northern Australia is increasingly altering the quantity, quality, timing, duration and frequency of freshwater flows to estuaries. There is increasing recognition of the need to allocate water for the environment as part of the sustainable use of water resources and to consider in a quantitative manner the impacts of water abstraction and regulation on downstream ecosystems (Davis and Hirji 2003 a,b,c; Dyson et al. 2003).

Results from the current study indicate that the impact of altering freshwater flows varies seasonally, with the greatest impacts on the growth rates of barramundi occurring during
summer, late spring and early autumn. This is an obvious, albeit previously unquantified, outcome for a species that has seasonal growth. In addition, altering freshwater flows will have greater consequences on the growth rates of smaller (younger) fish, whose instantaneous rate of growth is faster than that of larger (older) fish. It is difficult to make more detailed speculations of the consequences of altering flow on the production (i.e. fisheries catch) of estuary-associated species such as barramundi without further, more detailed modelling and the exploration of potential lagged effects of freshwater flow. However, more detailed modelling is an area of research that would potentially provide quantitative answers to the continuing questions that fisheries scientists are frequently asked by water managers; namely: (a) How much water do estuaries require? and (b) What are the consequences of altering the freshwater flow regime by a certain quantity at a certain time of year?