CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2011, **62**, 937–951

Spatial patterns in the demography of a large estuarine teleost: king threadfin, *Polydactylus macrochir*

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Abstract. Understanding spatial patterns in demographic parameters of exploited fish species is of critical importance to effective fisheries management. In the present study, patterns in demography of a large, protandrous, estuarine teleost, king threadfin, *Polydactylus macrochir*, were compared among three estuaries on the eastern coast of Queensland, Australia. Significant variation in age and growth was observed between fish from the Fitzroy River and those from the Mary and Brisbane Rivers, with Fitzroy River fish living longer (22 years *v.* 10 and 14 years, respectively), reaching a greater asymptotic length (1222-mm fork length (FL) *v.* 975- and 1047-mm FL, respectively), and attaining greater length-at-ages of 6 years and beyond. No difference in growth was detected between Mary and Brisbane River fish, or in total mortality among any of the sites. Fitzroy River fish were generally found to mature and change sex at greater lengths and ages than those from the Mary and Brisbane Rivers. The observed variability suggests that spatially segregated populations of *P. macrochir* may respond differently to fishing pressure and highlights the importance of understanding the spatial patterns in demography of exploited estuarine fish populations.

Additional keywords: Australia, fisheries management, growth, maturity, population biology, sex change.

Introduction

Understanding the demography of exploited fish species is of fundamental importance to the development of sustainable fisheries management. Demographic parameters such as growth patterns, maturity profiles and mortality rates are critical components in developing stock assessments and productivity models from which suitable harvest regimes and effective management strategies can be derived (Beverton and Holt 1957; Ricker 1975; Haddon 2001).

Typically, quantification of the key demographic parameters used in fisheries assessment models is based on samples pooled across a species distribution or management area, or from extrapolations made from fish from one particular area (Sale *et al*. 2006). For many species, the spatial variability of demographic parameters within management areas has received little attention from fisheries managers, mainly because of the high costs involved with the need for spatial assessment over typically large management areas and the difficulties associated with enforcing the boundaries for spatially explicit management controls (Kritzer and Sale 2006; Williams *et al*. 2006). However, the metapopulation structures exhibited by many exploited fish species may lead to high levels of demographic variation among populations within a management area (Kritzer and Sale 2006). Failure to take account of such differences in stock assessments and subsequent management arrangements may lead to over-exploitation of isolated populations, particularly of less productive stocks, whereas potential yields may not be realised for more productive components (Williams *et al*. 2006).

Numerous studies have documented variation in demographic parameters of tropical reef species across both large- and small-scale geographical areas (Kritzer 2002; Williams *et al*. 2006; Allman 2007; Paddack *et al*. 2009). In contrast, fewer studies have examined such patterns for tropical estuarine species. A growing body of evidence suggests that the biology of estuarine fishes is strongly linked to the environmental conditions of the habitats in which they reside, with positive associations between environmental factors such as freshwater flow and catch-per-unit effort (as a proxy for population abundance), growth and year-class strength reported for several species (e.g. Staunton-Smith *et al*. 2004; Robins *et al*. 2006; Halliday *et al*. 2008; Gillson *et al*. 2009). As such, considerable variation in demography among spatially isolated estuarine populations seems probable, particularly where differences in environmental conditions are pronounced. Given that estuarine fishes continue to face heavy fishing pressure and habitat alteration worldwide, it becomes increasingly important to determine spatial patterns of demography of exploited estuarine species, so as to establish sustainable harvest and optimal management practices.

10.1071/MF11034 1323-1650/11/080937

The king threadfin, *Polydactylus macrochir* Günther, 1867 (Polynemidae), is a protandrous teleost that inhabits estuaries and turbid coastal waters across northern Australia and southern Papua New Guinea (Motomura *et al*. 2000), where it supports important commercial, recreational and artisanal fisheries. On the eastern coast of Queensland, Australia, the species forms an important component of the multi-species commercial inshore net fishery, being the second-most important target species after the barramundi, *Lates calcarifer* Bloch, with a reported 108 t harvested in 2005 (Queensland Department of Primary Industries and Fisheries 2007). Concern currently exists for the health of Australia's *P. macrochir* stocks, with populations in Western Australia considered over-exploited (Pember *et al*. 2005). There is evidence of overfishing of *P. macrochir* in the waters of the Gulf of Carpentaria in Queensland, with significant age truncation and reductions in length and age at sex change compared with samples collected 10–15 years ago (Moore *et al*. 2010).

Although previous studies have provided preliminary estimates for some demographic parameters of *P. macrochir* in the waters of the eastern coast of Queensland (Russell 1988) and elsewhere across northern Australia (Bibby and McPherson 1997; McPherson 1997; Pember *et al*. 2005), spatial differences in demography have not been examined. In the present study, spatial patterns in demography, including growth, mortality, length and age at maturity and length and age at sex change, were examined among three geographically distinct populations on the eastern coast of Queensland. Given their isolation, it was hypothesised that the populations would exhibit significant differences in demography.

Materials and methods

Study sites

Samples of *Polydactylus macrochir* were collected from the estuarine reaches of the Fitzroy, Mary and Brisbane Rivers in central and south-eastern Queensland between July 2007 and March 2010 (Fig. 1). These rivers differ considerably in catchment size, surrounding land use and fishing pressure. The Fitzroy River is the largest river on the eastern coast of

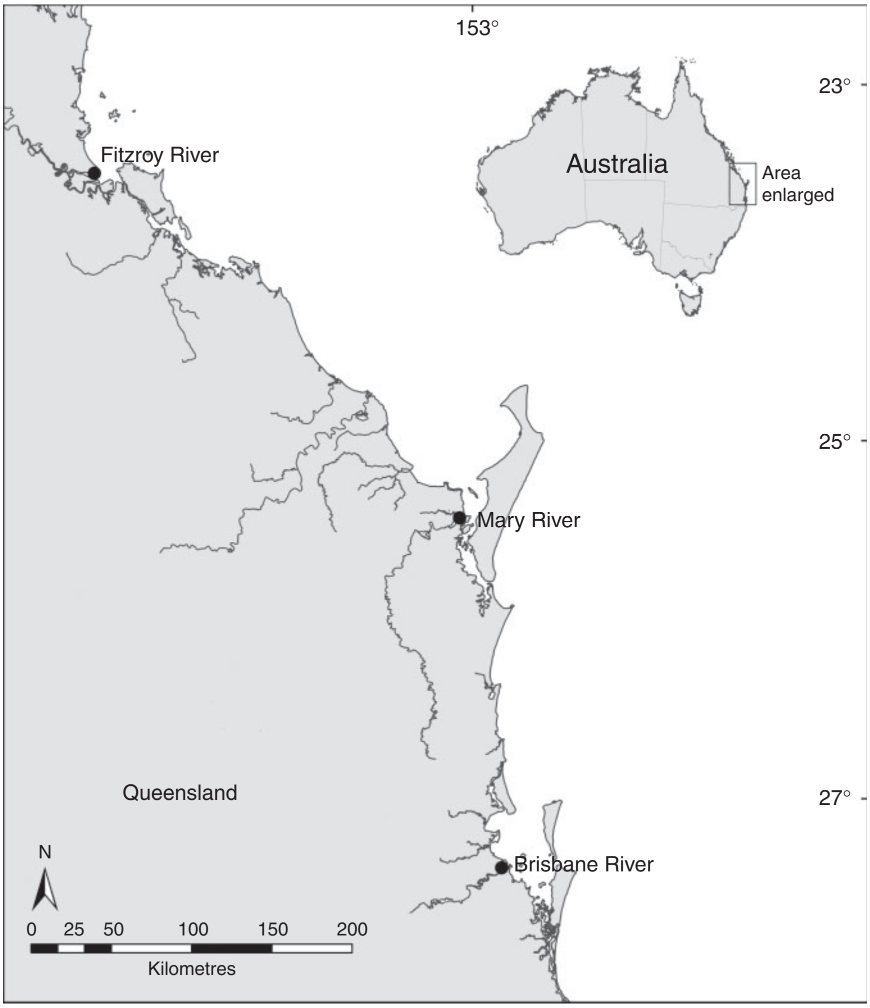

Fig. 1. The central and south-eastern Queensland coast, showing the three sampling sites used in the study.

Queensland, with a catchment of 142 500 km^2. A tidal barrage occurs on the river at the city of Rockhampton (~50 km from the river mouth) which delineates the upper limit of the estuary. The lower reaches of the Fitzroy River estuary are extensively channelised, with substantial areas of mangrove, intertidal salt marshes and salt pans (Long and McKinnon 2002). The estuarine reaches support the largest fishery for *P. macrochir* on the eastern coast of Queensland, with ~22 t harvested in 2005 (Queensland Department of Industries and Fisheries 2007).

The Mary River has a catchment of ~9595 km^2. A tidal barrage occurs ~60 km upstream from the mouth. The lower reaches of the Mary River estuary have extensive areas of mangrove, intertidal salt marshes and extensive salt pans. The Mary River estuary supports a small, yet significant fishery for *P. macrochir*, with 11.8 t harvested in 2005 (Queensland Department of Industries and Fisheries 2007).

The Brisbane River has a catchment of ~13 500 km^2. The tidal influence of the Brisbane River estuary ceases at Mount Crosby Weir, ~80 km upstream from the mouth. Dredging and removal of width restrictions associated with port development and maintenance have deepened and widened the lower estuarine reaches, reducing the amount of mangrove habitat and changing the tidal range, tidal prism, and ebb and flood tide velocities of the estuary (Dobson 1990). Although no commercial fishing for *P. macrochir* occurs in the Brisbane River, the species is a popular target for local recreational anglers.

Sample collection

Samples from the Fitzroy and Mary Rivers were obtained while onboard commercial vessels and/or from fish processors, whereas Brisbane River samples were collected through a fishery-independent sampling program by using the same gear as used by commercial fishers (i.e. gill-nets of 4–6.5-inch (100 mm to 165 mm) mesh diameter) ($n = 34$), by opportunistic collections from recreational fishers ($n = 42$), and by research line-fishing ($n = 9$). The total length (TL), length to caudal fork (FL) and upper jaw length (UJL) were measured to the nearest millimetre for each individual fish collected unless damaged. Although whole weights (W_w) were generally unavailable from fishery-processor-sourced samples because these had been filleted before biological processing, whole weights, measured to the nearest 1 g, were available for the majority of Brisbane River specimens. Sagittal otoliths (hereafter referred to as otoliths) were removed for all specimens, cleaned, dried and stored in paper envelopes, until processing in the laboratory. Sex and maturity stage was determined from a macroscopic examination of the gonads (Table 1). Because some samples were eviscerated at sea, it was not possible to determine sex and maturity stage for all specimens. Although fishery controls for the species are based on TL, we have analysed and presented FL data, because the fishery-sourced samples frequently had damage to the distal margins of the tail, precluding accurate TL measurements for some specimens.

Age determination

A comparison of whole- and sectioned-otolith reads was conducted to assess which structure would be used for ageing.

Table 1. Descriptions used to macroscopically stage the development of *Polydactylus macrochir* gonads (adapted from Pember *et al.* 2005)

Stage	Description	Testes	Ovaries
I/II	Immature/resting	Small, grey and strand-like (Stage I) to white and ribbon-like (Stage II).	Small and transparent. Yellowish-orange in colour. Oocytes not visible through ovarian wall.
III	Developing	White and occupy approximately half the length of body cavity.	Slightly larger than Stage II. Oocytes visible through ovarian wall.
IV	Maturing	No milt appears when pressure is applied to trunk of males. Occupy more than half the length of the body cavity.	Larger than Stage III, occupying half of body cavity. Creamy orange in colour. Large oocytes visible through ovarian wall.
V/VI	Ripe/running ripe	One-third to filling body cavity. Milt exuded with firm pressure to abdominal cavity (Stage VI).	Large, occupying half to two-thirds of body cavity. Extensive capillaries visible in ovarian wall. Hydrated oocytes sometimes visible through ovarian wall in Stage VI ovaries. Ovaries typically with anterior lateral undulations.
VII	Spent	Smaller than Stage V or VI. Gonads flaccid but not totally empty.	Smaller than Stages V and VI and flaccid. Some large oocytes visible through ovarian wall.
VIII	Recovering	Red to brown, small and flaccid.	Small, flaccid and dark red.

Whole otoliths from a total of 460 individuals, taken from fish samples across all sites and length classes (including an additional 242 samples collected from the Fitzroy River between 2000 and 2005), were immersed in oil and examined microscopically under a reflected light against a black background and the number of opaque zones was counted. For otoliths from larger individuals, it was necessary to rotate the otolith to observe the annuli towards the otolith margin.

The same otoliths were mounted in resin and up to four transverse sections 300 µm thick each were taken with a slow-speed diamond-edged saw (Buehler Isomet, Lake Bluff, IL, USA). Care was taken to ensure the primordium of the otolith was included in at least one section. All sections were cleaned and mounted on glass microscope slides with polyester resin. Otolith sections were examined under a stereo dissecting microscope, with reflected light against a black background.

An image of each whole and sectioned otolith was taken with a DC 300 digital camera (Leica, Wetzlar, Germany) connected to the dissecting microscope. Ages of both whole and sectioned otoliths were assigned on the basis of counts of alternating opaque and translucent bands, verified as annuli by Pember *et al.* (2005). To assess the timing of annuli formation at each site, the margin of each otolith was classified into one of the following four categories: (1) continuous opaque band formed around the edge of otolith, with no translucent material beyond the last opaque band; (2) translucent band laid onto the outer edge, comprising less than half the width of the previous translucent band; (3) translucent band laid onto the outer edge, comprising roughly half or more the width of the previous translucent band; and (4) opaque band on the edge of the otolith; however, band is not continuous.

The precision of annuli estimates from whole and sectioned otoliths was calculated using the coefficient of variation (CV) (Chang 1982). Greater precision is achieved when CV is minimised (Campana *et al.* 1995). Once the method of reading was established (see Results), each otolith was read twice. When counts did not agree, a third reading was taken, and if two counts agreed, they were accepted as the number of annuli. When all three counts differed, the otolith was rejected from further analysis. All otoliths were read by a single, experienced reader (BRM) whose reading accuracy was tested against a reference set of *P. macrochir* otoliths. Otoliths used in the reference set were collected from the Fitzroy River between October 2000 and February 2005. Counts from this reader were considered valid on the basis of a consistent agreement with counts of the reference otoliths.

The absolute age of each individual fish was estimated from the number of annuli, the assumed birth date, the estimated date of annuli deposition and the date of capture. The advantage of including the annual fractions elapsed between the estimated birth date and the time of annuli deposition, and the time of annuli deposition and the date of capture is that this avoids any potential bias in age estimates resulting from spatio-temporal variations in spawning season and time of annuli deposition or variations in the date of capture. Birth dates were estimated as 1 November from the peak of the spawning period (see Results). A common date of annuli completion of 31 October was assumed for fish from all sites, years and age classes, consistent with the marginal increment trends for *P. macrochir* at each site (see Results). The ageing algorithm took the following form:

$$age_{\mathrm{m}} = ((n-1) \times 12) + m_{\mathrm{b}} + m_{\mathrm{c}},$$

where age_{m} is the age in months, n is the number of annuli, m_{b} is the number of months from the assigned birth date to the date of annuli completion (i.e. 1 November to 31 October), and m_{c} is the number of months from the date of annuli completion to the date of capture. Ages were then converted to a yearly fraction by dividing the age in months by 12. Adjusted age estimates were rounded to the nearest year for estimation of age frequency distributions and age at maturity and sex change.

Morphometrics

The relationships between FL and UJL, and FL and TL, were determined for each site by a linear function. Relationships were compared among sites by using analysis of covariance (ANCOVA), with FL being the covariate. Length data were log-transformed before analysis to satisfy the assumptions of normality and homogeneity of variances.

The relationship between FL and whole weight (where available) was described by a power function of the following form:

$$W_{\mathrm{w}} = a\mathrm{FL}^{\mathrm{b}},$$

where W_{w} is the whole-fish weight (g), FL is the fork length (mm), a is the coefficient of the power function and b is the exponent. Additional young-of-the year fish samples collected from the Fitzroy River in 2003 ($n = 5$) were used to help determine the length–weight relationship.

Age, growth and mortality

Growth of *P. macrochir* was modelled at each site by using the von Bertalanffy growth function (VBGF) fitted with non-linear least-squares regression of FL on age. Because *P. macrochir* is protandrous, a single VBGF was fitted for both males and females. The form of the VBGF used to model length-at-age data was as follows:

$$L_t = L_\infty [1 - e^{-K(t-t_0)}],$$

where L_{t} is the length-at-age, L_∞ is the hypothetical asymptotic length, K is the growth coefficient, and t_0 is the hypothetical age at which fish would have zero growth. VBGFs were compared among sites by using likelihood-ratio tests. A common range of age classes (2–10 years) was used in each analysis to assure validity of the comparisons (Haddon 2001).

Statistical comparisons of the VBGF model can be problematic because the model is strongly determined by the values for L_∞ and t_0, which are at the extremes of the curve and often have the least data (Haddon 2001). Because of such sensitivities, spatial patterns in growth were also examined through an analysis of mean length-at-age. One-way analysis of variance (ANOVA) was used to test for differences in mean length-at-age among sites for each common age class, using site as a fixed factor in the univariate design. Shapiro Wilk tests revealed that the length data for most age classes were non-normally

Table 2. Summary of *Polydactylus macrochir* collected from three estuaries on the eastern coast of Queensland, Australia

Site	*n*	Age range (years)	FL range (mm)	*n* (males)	*n* (females)	*n* (transitionals)	*n* (undetermined)
Fitzroy River	699	1.7–21.9	430–1354	241	29	6	423
Mary River	61	2.0–10.9	440–1016	47	8	1	5
Brisbane River	85	1.8–13.8	493–1062	58	18	2	7

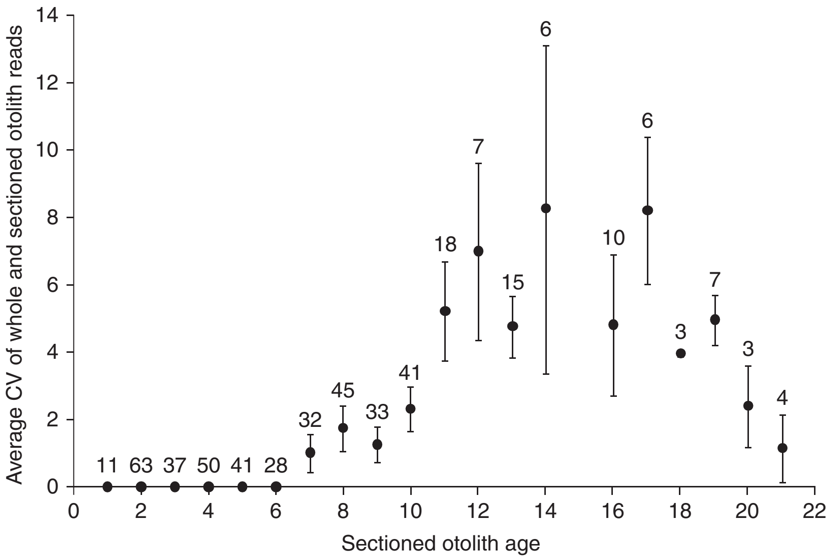

Fig. 2. Coefficient of variation (CV) (±s.e.) for annuli estimates between whole and sectioned otoliths plotted against counts of annuli from sectioned otoliths of *Polydactylus macrochir*. Numbers above error bars indicate sample size.

distributed ($P < 0.05$); so, to satisfy assumptions of normality and homogeneity of variances, the data were log-transformed before analysis. Significant results were examined using Tukey–Kramer *post hoc* pair-wise comparisons (Sokal and Rohlf 1995).

Total instantaneous mortality rates (Z) were estimated for each estuary by age-based catch curves (Ricker 1975), where the frequency of fish in each age class was log-transformed ($\ln(x+1)$) and regressed against the corresponding age. Z was estimated as the absolute value of the regression slope, b. Catch curves were fitted for all fully recruited age classes, defined as those age classes that were greater than or equal to the modal age class in the sample. Estimates of Z were compared across estuaries by analysis of covariance (ANCOVA), with age as the covariate.

Reproductive biology

The spawning season for *P. macrochir* at the three sites was estimated on the basis of macroscopic staging of reproductive tissue samples and by the gonado-somatic index (GSI). The GSI was calculated for each male fish with a FL greater than the estimated length at 50% maturity (L_{m50}) and for each mature female fish (Stage III or above) using the following equation:

$$GSI = \left(\frac{W_g}{W_W}\right) \times 100,$$

where W_g is gonad weight and W_w is the whole-fish weight. For several fish individuals, only one complete gonad lobe was available, as a result of damage during processing. Analysis of 50 randomly sampled gonads revealed no statistically significant difference between the weight of the left and right lobe (one-way ANOVA, $P < 0.05$). Consequently W_g was estimated by multiplying the weight of the single complete lobe by two. Because measurements of W_w were generally unavailable from the Fitzroy or Mary River samples, W_w was estimated for these fish individuals by using the length–weight relationship established on the basis of samples predominately from the Brisbane River. It was assumed that estimates of W_w derived from this relationship would suffice for use in estimating GSI values because only the temporal patterns in GSI, rather than absolute values, were examined to determine spawning season. Mean monthly GSI values and the proportion of individuals in each macroscopically determined reproductive stage were plotted separately for males and females to determine the seasonality of spawning in the eastern-coast populations of *P. macrochir*. Because preliminary results revealed no significant difference in the peak or duration of spawning among the sites, the GSI and staging data were pooled across sites to maximise samples sizes for each month.

The length and age at maturity was determined for samples of male fish on the basis of the macroscopic stage assessments (Table 1). Fish with gonads staged III–VIII were defined as mature. Individuals assigned a gonad stage of I or II were defined as immature, because they were considered incapable of spawning during the upcoming spawning season. To reduce the probability of mis-identifying post-spawning gonads as immature, only fish samples collected immediately before or during the spawning season or those that were obviously mature (i.e. milt present) were used to calculate the length and age at sexual maturity.

The length and age at which 50% of *P. macrochir* population attains maturity for each of the sites was determined by logistic regression analysis, using the following equation:

$$Pm = 1/[1 + \exp(-\ln(19)(m - m_{50})/(m_{95} - m_{50}))],$$

where Pm = the proportion of mature fish in each age or 50-mm FL class (m), m_{50} and m_{95} are the lengths or ages at which 50% and 95% of the population is mature, respectively. The data were randomly resampled and analysed to create 500 sets of bootstrap estimates for the parameters of the logistic equation and estimates of the probability of maturity within the recorded lengths and ages. The point estimates for each parameter and of each probability of maturity were taken as the medians of the bootstrap estimates. Approximate 95% confidence limits of the parameters were calculated as the 2.5 and 97.5 percentiles of the parameter estimates obtained from the resampling technique. A second logistic regression analysis, of the form described above, was used to estimate the length and age at which 50% of *P. macrochir* population changed sex across the three estuaries. Non-overlapping confidence intervals were used to indicate significant differences in the length and age at 50% maturity and sex change among sites.

Results

In total, 845 *P. macrochir* individuals were collected from the three sites. Female fish were uncommon at all sites, comprising 10.5%, 14.3% and 23.1% of the samples with gonads present from the Fitzroy, Mary and Brisbane Rivers, respectively (Table 2). No significant difference was observed in length-at-age within common age classes collected by the fishery-independent methods and the recreationally sourced fish from the Brisbane River (Age classes 3–7 and 11, one-way ANOVA, $P \geq 0.118$), or between the overall lengths ($F_{1,83} = 0.189$, $P = 0.665$) or ages ($F_{1,82} = 2.904$, $P = 0.092$) of fish caught with the two methods; hence, these samples were pooled to maximise sample sizes for analysis.

Age determination and timing of annuli deposition

The CV of age estimates between whole and sectioned otoliths was 1.22% (averaged across all ages), indicating a high degree of precision between whole- and sectioned-otolith age estimates. However, when analysed against age, there was an increasing divergence in age estimation between whole and sectioned otoliths as the number of annuli increased, particularly for otoliths with 7–17 annuli (Fig. 2). In general, whole otoliths provided an underestimation of age compared with sectioned otoliths. The apparent increase in accuracy in whole reads of fish with 18 or more annuli is likely to be due to the small sample sizes in the age classes, and an awareness of the maximum age of the species. All otoliths were initially read whole. Otoliths in which six or fewer annuli were counted in the initial read were read whole again, whereas otoliths in which more than six annuli were counted in the initial read were sectioned before being read again.

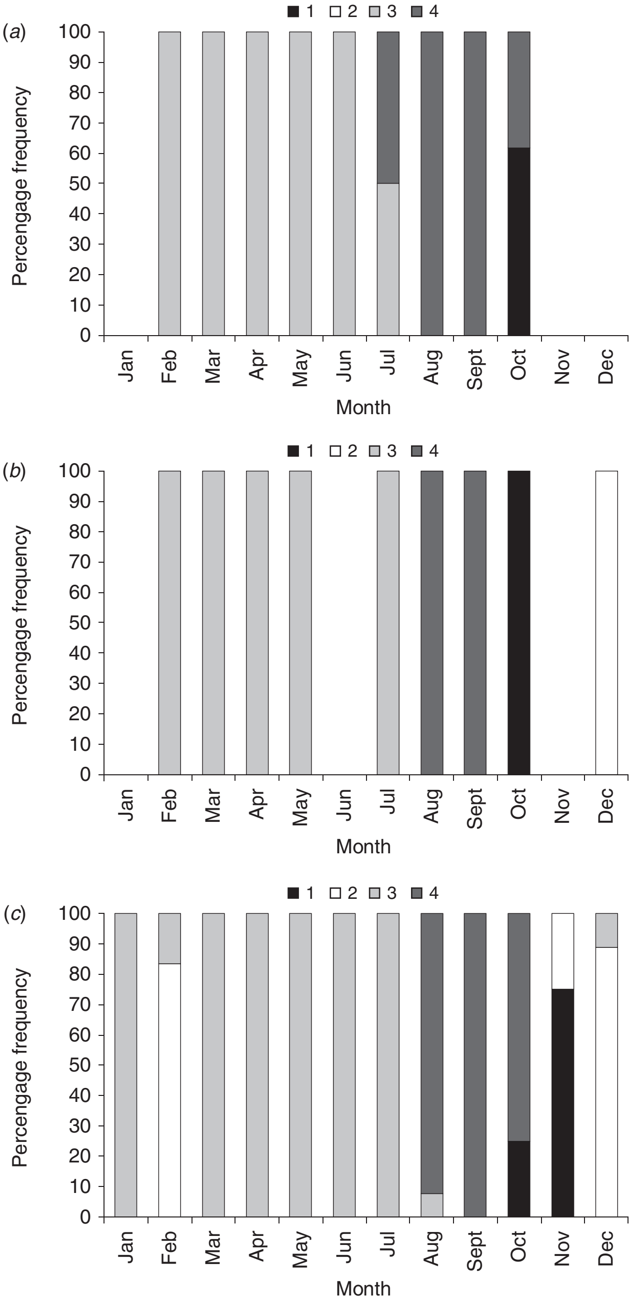

Fig. 3. Percentage of *Polydactylus macrochir* otoliths in each marginal edge category from the (*a*) Fitzroy, (*b*) Mary and (*c*) Brisbane Rivers on the eastern coast of Queensland, Australia.

Examination of the otolith marginal increment revealed consistent trends in the timing of annuli deposition across the sites (Fig. 3). Otoliths collected between December and July from all sites had translucent margins. Non-continuous bands were generally observed in samples collected between August and October, whereas newly formed completed bands were observed in fish collected in October and November. These results suggest that annuli deposition is completed by the beginning of November at each of the sites.

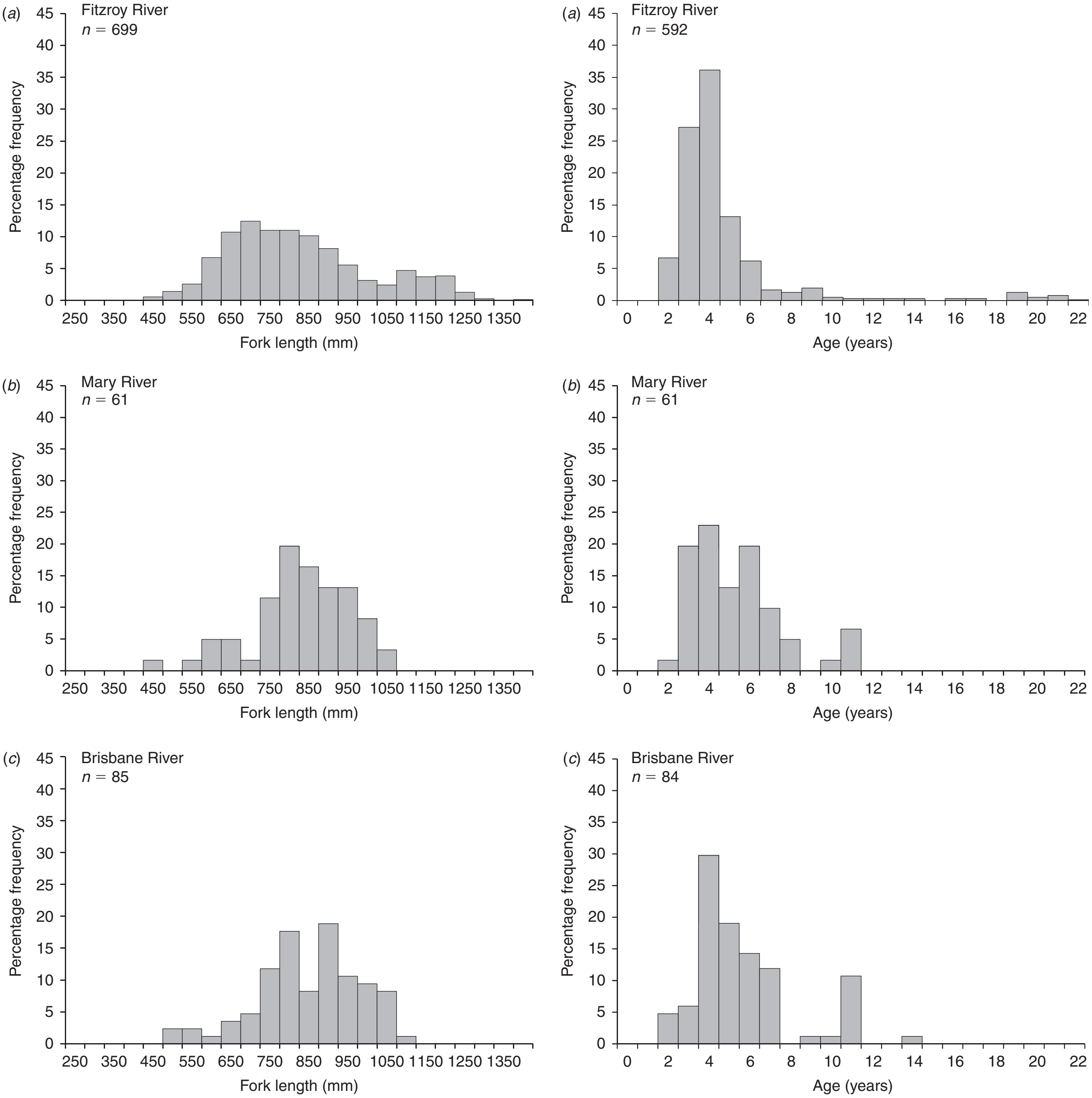

Fig. 4. Length and age frequency distributions for *Polydactylus macrochir* from the Fitzroy, Mary and Brisbane Rivers.

Morphometrics

There was no significant difference in the relationship between UJL and FL or FL and TL between sites (ANCOVA, $F_{2,819} = 0.74, P = 0.48$, and $F_{2,631} = 0.96, P = 0.38$, respectively). The relationship between UJL and FL, combined across all sites, was $\mathrm{FL} = 8.3115\mathrm{UJL} - 27.317$ ($r^2 = 0.92$, $n = 822$). The relationship between FL and TL was $\mathrm{TL} = 1.1737\mathrm{FL} + 22.083$ ($r^2 = 0.99$, $n = 635$). The relationship between FL and W_w was isometric: $W_\mathrm{w} = 2.00 \times 10^{-5} \times \mathrm{FL}^{2.9326}$ ($r^2 = 0.99$, $n = 73$).

Length and age structure

The modal length of *P. macrochir* individuals differed among sites, and was largest for the Brisbane River, smallest for the Fitzroy River, and intermediate for the Mary River (Fig. 4). Fish from the Fitzroy River grew to greater lengths than those from the Mary or Brisbane Rivers, with a maximum FL of 1354 mm recorded. The modal age of *P. macrochir* was 4 years for each estuary. The maximum age from the Fitzroy River (21.9 years) considerably exceeded those

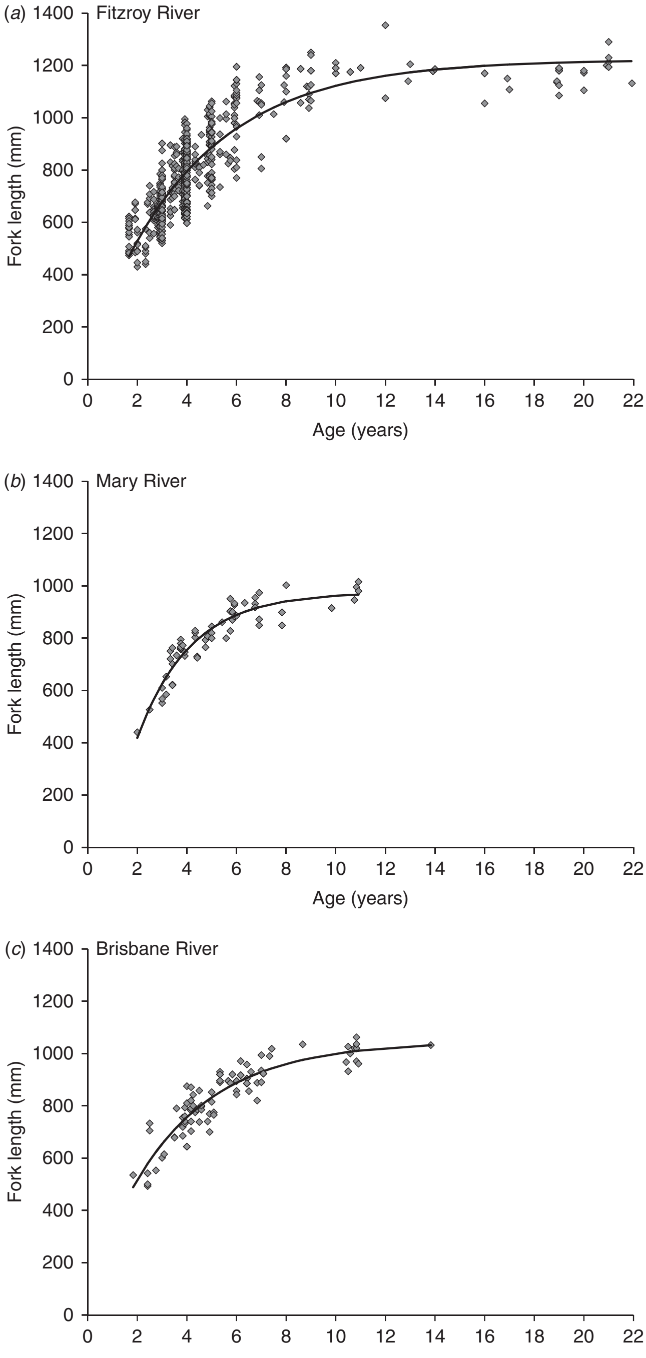

Fig. 5. von Bertalanffy growth curves fitted to length-at-age data from *Polydactylus macrochir* from the (*a*) Fitzroy, (*b*) Mary and (*c*) Brisbane Rivers, Queensland, Australia.

of the Mary (10.9 years) and the Brisbane (13.8 years) Rivers (Table 2).

Age, growth and mortality

There was substantial variation in von Bertalanffy growth curves for *P. macrochir* across the sites (Fig. 5, Table 3). Likelihood-ratio tests indicated that the pattern of growth of fish from the Fitzroy River differed significantly from that of fish from the Mary and Brisbane Rivers ($\chi^2 = 24.42$, d.f. = 3, $P < 0.0001$, and $\chi^2 = 17.49$, d.f. = 3, $P = 0.0006$, respectively), with Fitzroy River fish reaching a greater L_∞. No difference in growth was observed between the Mary and Brisbane River samples ($\chi^2 = 6.75$, d.f. = 3, $P = 0.08$).

Table 3. von Bertalanffy growth parameters and rates of total mortality for *Polydactylus macrochir* from three estuaries on the eastern coast of Queensland, Australia

Site	L_∞ (mm)	K	t_o	Z
Fitzroy River	1222	0.24	–0.34	0.119 ($r^2 = 0.49$)
Mary River	975	0.46	0.79	0.311 ($r^2 = 0.46$)
Brisbane River	1047	0.30	–0.25	0.298 ($r^2 = 0.55$)

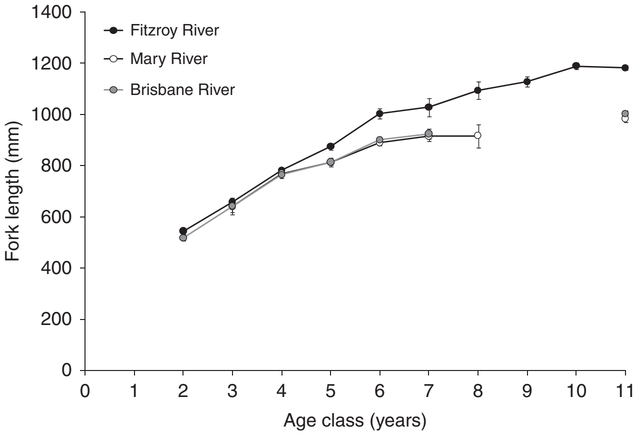

Fig. 6. Mean length-at-age (±s.e.) for *Polydactylus macrochir* from three estuaries on the eastern coast of Queensland, Australia. Only age classes with two or more data points are displayed.

No significant difference in mean length-at-age was detected between fish from the Mary and Brisbane Rivers for any age class, or between samples from the Fitzroy River and Mary and Brisbane Rivers for Age classes 2–5 years (Fig. 6). Fish from the Fitzroy River were generally larger than those from the Mary River for common age classes (Age classes 6, 8 and 11; $P = 0.003$, $P = 0.016$ and $P < 0.001$, respectively) and the Brisbane River (Age classes 6, 7 and 11; $P = 0.009$, $P = 0.043$ and $P < 0.001$, respectively).

Estimates of total mortality (Z) were highest for the Mary River and lowest for the Fitzroy River (Table 3). No significant difference in Z was detected among sites (ANCOVA, $F_{2,34} = 3.14$, $P = 0.057$). A poor overall fit of the catch-curve regressions was observed at each site (Table 3).

Reproductive biology

The mean monthly GSIs for male *P. macrochir* rose gradually from a low in June and July to reach a maximum in November, and then declined over the ensuing 4 months (Fig. 7). Ripe (Stage V) males were present in samples collected from September to February, and running ripe (Stage VI) males were

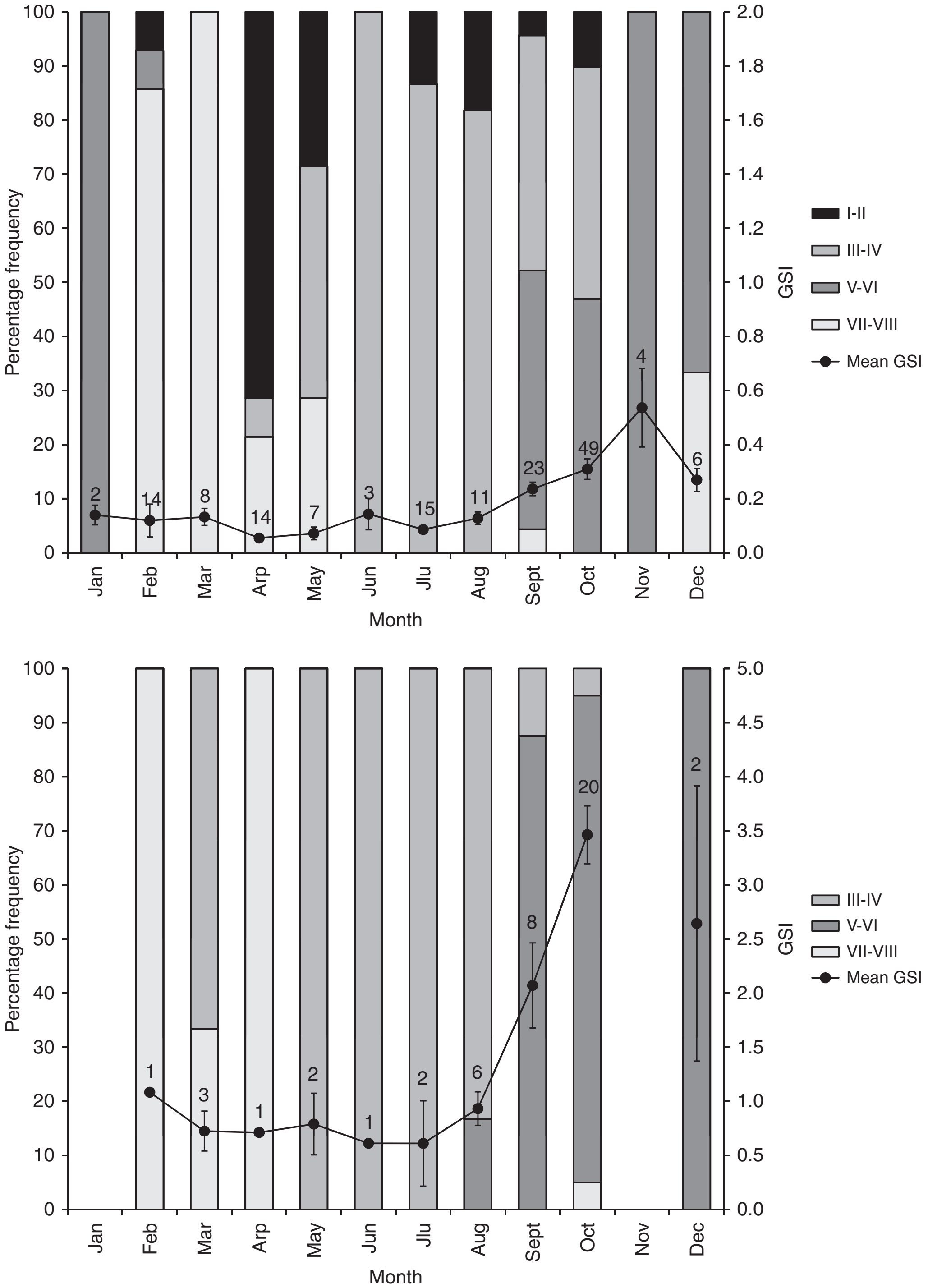

Fig. 7. Monthly macroscopic gonad stages and mean gonado-somatic index (GSI) values (±s.e.) for (*a*) male and (*b*) female *Polydactylus macrochir* from the eastern coast of Queensland, Australia. Numbers above error bars indicate sample size.

observed in samples collected from October to January. The majority of spent males were observed in December, February and March, although a few spent males were observed in April (Fig. 7), suggesting that spawning activity may have continued until at least March.

The mean monthly GSI for females rose sharply from a low in July to high levels in October and December (Fig. 7). In addition, most females with ripe and running ripe ovaries were present in samples collected from August–October and December (Fig. 7). Females with ovaries containing hydrated oocytes,

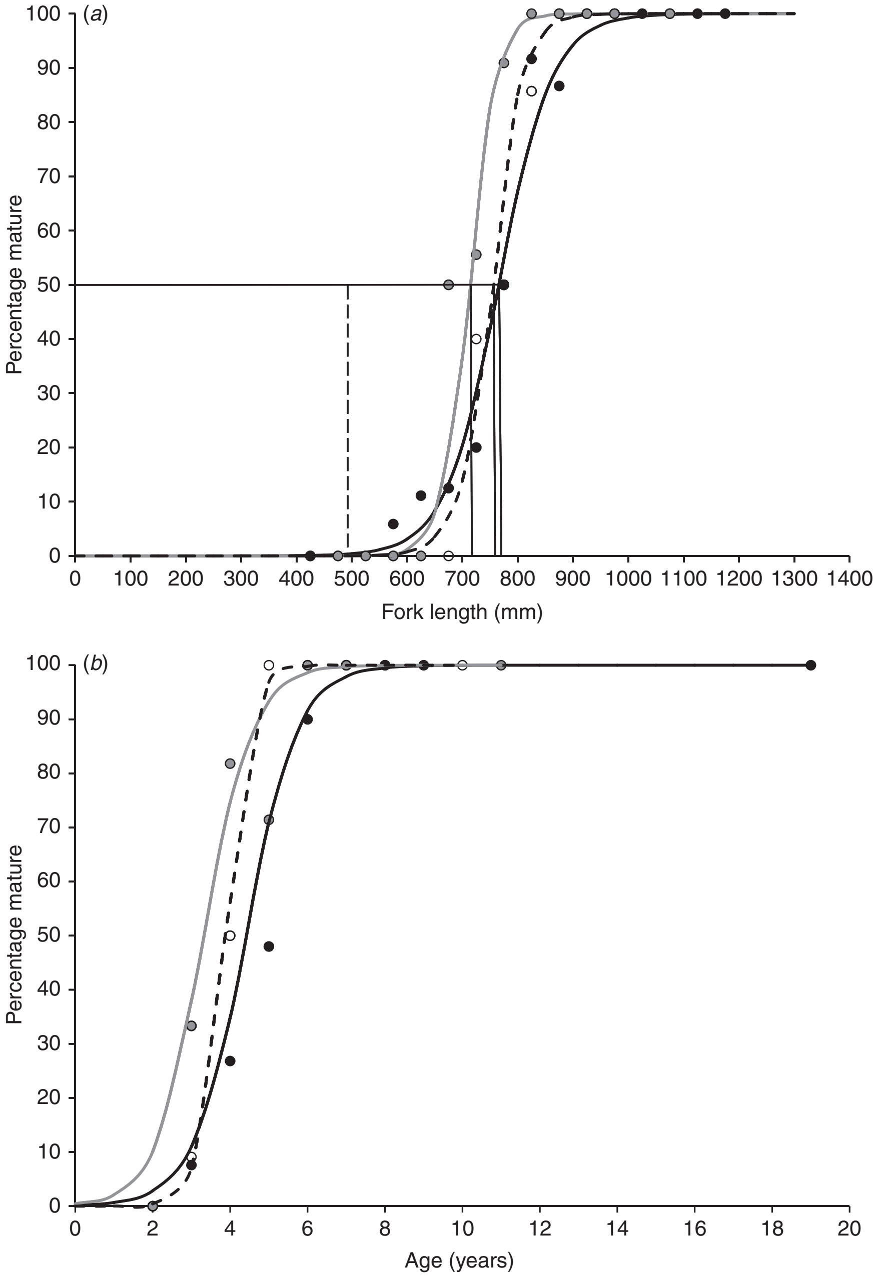

Fig. 8. Logistic curves showing (*a*) length and (*b*) age at maturity for male *Polydactylus macrochir* individuals from Fitzroy (black line, solid circles), Mary (dashed line, open circles) and Brisbane (grey line, grey circles) Rivers. The solid black vertical lines represent the lengths at which 50% of the male populations are mature (i.e. L_{m50}) for each site, and the dashed vertical line indicates the current minimum legal length (49-cm FL (= 60-cm TL)).

indicative of active spawning, were sampled only in October and December. There were no females collected in November or January from any of the three sites, precluding the verification of whether females spawned in these months. However, because of the elevated GSI values in the preceding and following months, it is likely that female GSI values remained high during these months. On the basis of these trends in GSI and monthly frequencies of ovarian and testicular stages, it was concluded that *P. macrochir* spawns between October and March at each site on the eastern coast of Queensland, with peak spawning occurring between October and December.

The estimated length and age at which 50% of male fish are mature (i.e. L_{m50} and A_{m50}) were lowest for the Brisbane River (710-mm FL, 3.3 years old), intermediate for the Mary River (755-mm FL, 3.9 years) and highest for the Fitzroy River (765-mm FL, 4.4 years old) (Fig. 8, Table 4). Although overlapping confidence intervals indicated that there were no significant differences in length at 50% maturity between the Fitzroy and

Table 4. Length and age at 50% of maturity (L_{m50}, A_{m50}, respectively) and sex change (L_{s50}, A_{s50}, respectively) and 95% confidence intervals for male *Polydactylus macrochir* from three estuaries on the eastern coast of Queensland, Australia

CI, confidence interval

Site	Fork length (mm)		Age (years)	
	L_{m50} or L_{s50}	95% CI	A_{m50} or A_{s50}	95% CI
Maturity				
Fitzroy River	765	743–788	4.4	4.2–4.7
Mary River	755	723–785	3.9	3.2–4.1
Brisbane River	710	677–740	3.3	2.7–3.8
Sex change				
Fitzroy River	1140	1082–1234	9.7	8.4–12.6
Mary River	960	925–1053	8.3	7.1–9.8
Brisbane River	932	912–959	7.5	6.5–8.9

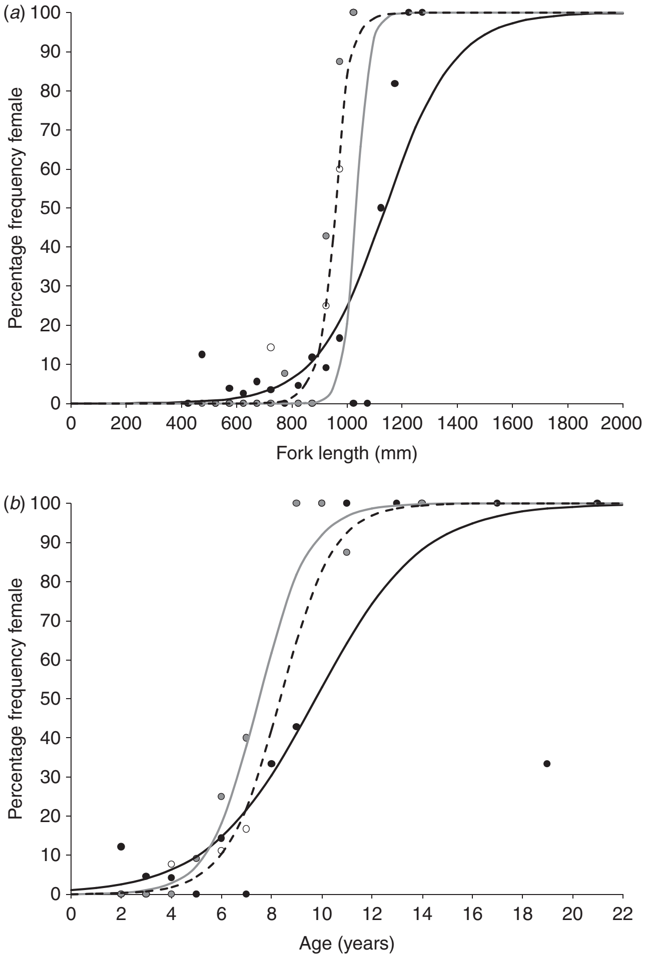

Fig. 9. Logistic curves showing (*a*) length and (*b*) age at sex change for *Polydactylus macrochir* from the Fitzroy (black line, solid circles), Mary (dashed line, open circles) and Brisbane (grey line, grey circles) Rivers.

Mary Rivers, or the Mary and Brisbane Rivers, the length at 50% maturity of fish from the Brisbane River was significantly lower than that from the Fitzroy River (Table 4). Estimates of the length at 50% maturity from all sites were considerably greater than the current minimum legal size of 49-cm FL (converted from 60-cm TL). Age at 50% maturity was significantly higher for Fitzroy River fish than for fish from the Mary or Brisbane Rivers (Table 4). Mary and Brisbane River fish did not differ, as evidenced by the overlapping confidence intervals (Table 4).

The estimated length at which 50% of fish are female (i.e. L_{s50}) was lowest for the Brisbane River (932-mm FL) and highest for the Fitzroy River (1140-mm FL) (Fig. 9, Table 4). The L_{s50} of fish from the Fitzroy River was significantly higher than those from the Mary or Brisbane Rivers. No difference was observed in the L_{s50} of fish between the Mary and Brisbane Rivers (Table 4).

The estimated age at which 50% of the population was female (i.e. A_{s50}) was generally lowest for the Brisbane River (7.5 years) and highest for the Fitzroy River (9.7 years) (Fig. 9, Table 4). Whereas all fish individuals >11 years from the Mary and Brisbane Rivers were females, two 19-year-old males were observed from the Fitzroy River. Overlapping confidence intervals indicated no significant differences in the A_{s50} estimates among the sites.

Discussion

All demographic traits of *P. macrochir* examined in the present study, except total mortality and age at sex change, differed among the estuaries. Such variation suggests that spatially segregated populations of *P. macrochir* may respond differently to fishing pressure if managed as a single entity and may therefore require spatially distinct management arrangements.

It is unlikely that the observed spatial patterns in demography were caused by differences in the sampling methods. Gear-selectivity patterns and size-selective fishing practices often produce bias in length-at-age estimates (Sinclair *et al.* 2002; Taylor *et al.* 2005) and, therefore, can have a considerable effect on demographic comparisons. Gill-nets are highly selective and generally capture the larger individuals of a particular age class (Hilborn and Walters 1992). Begg and Sellin (1998) found differences in length-at-age between line- and net-caught school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*), with net-caught fish generally being larger than line-caught fish for any given age. Lucena and O'Brien (2001) observed significant differences in length-at-age of bluefish (*Pomatomus saltatrix*) between harvest methods, with gill-nets generally selecting for larger individuals in Age classes 1 and 2, than purse seine or trawl methods. In the present study, no significant difference was observed in length-at-age between net-caught and recreationally caught samples from the Brisbane River, suggesting little effect of size selectivity between netting and recreational fishing methods at this site.

Although the sample sizes varied markedly among sites, it is unlikely that these differences affected the comparisons of VBGF parameters or mean length-at-age, because these analyses were conducted on common age classes across the three sites. Similarly, the unequal sample sizes are factored into the development of the 95% confidence intervals for the comparisons of length and age at maturity and sex change, and thus are unlikely to confound these comparisons.

Age, growth and mortality

Significant variation in both mean length-at-age and VBGF parameters were observed between samples from the Fitzroy River and the Mary and Brisbane Rivers, with Fitzroy River fish generally attaining greater lengths for ages ≥ 6 years. It is unclear whether the observed differences in growth solely reflect genetic differentiation among populations, or result from differences in environmental factors among sites. *P. macrochir* from the Fitzroy and Brisbane Rivers are genetically distinct (Horne *et al.* 2010); however, little is known of their relationship to Mary River fish. Alternately, several exogenous factors may be responsible for the observed differences in growth, including inter- and intra-specific competition (Jones 1987), population size and/or density (Doherty 1983; Doherty and Fowler 1994), habitat and food availability (Weatherley and Gill 1987; Hart and Russ 1996), freshwater flow regimes (Staunton-Smith *et al.* 2004; Robins *et al.* 2006; Halliday *et al.* 2008), water temperature (Conover 1992; Durieux *et al.* 2009; Tolan and Fisher 2009; Brunel and Dickey-Collas 2010) or exploitation effects (Ricker 1981; Law 2000; Hilborn and Minte-Vera 2008). The greater lengths-at-age and subsequent greater lengths at maturity and sex change obtained by fish from the Fitzroy River, which supports the largest fishery for *P. macrochir* on the eastern coast of Queensland, suggests that fishing pressure is unlikely to be the sole cause of the observed spatial differences.

Despite the observed spatial variation, some generalisations about age and growth of *P. macrochir* on the eastern coast of Queensland can be drawn. *P. macrochir* populations in central and southern Queensland grow relatively rapidly early in life, generally attaining mean lengths of ~540-mm FL after 2 years of life. In contrast, *P. macrochir* populations in Western Australia attain lengths of only 370-mm FL after 2 years (Pember *et al.* 2005). The maximum observed age of 22 years for *P. macrochir* in the Fitzroy River was considerably higher than those reported for the species elsewhere in Australian waters, and for any other species of polynemid worldwide. Pember *et al.* (2005) reported a maximum age of 10 years for *P. macrochir* in Western Australia, whereas Bibby and McPherson (1997) reported a maximum age of 14 years for *P. macrochir* in the waters of Gulf of Carpentaria in Queensland. Such marked differences in maximum ages among regions may reflect differences in fishing pressure and suggest that *P. macrochir* populations in north-western Western Australia and the Gulf of Carpentaria may be more heavily exploited than those in central and southern Queensland.

There was a conspicuous absence of fish <2 years old in the samples. This is most likely a result of selectivity of the sampling gear used, rather than the existence of separate juvenile and adult habitats. Juveniles of *P. macrochir* have been observed to be broadly distributed in estuaries, and are commonly observed in the stomachs of adult fish (Pember 2006; B. Moore, pers. obs.), suggesting overlap in their distributions. The exclusion of fish <2 years old from estimates of growth using the VBGF may result in an underestimation of K and a corresponding overestimation of L_∞ (Ferreira and Russ 1994; Williams *et al.* 2007). Nevertheless, it is likely that the absence of fish <2 years old had little effect on the growth comparisons, owing to the presence of fish larger than the estimated L_∞ at all sites and the similarity in the range of age classes sampled among estuaries.

Although no difference in mortality was observed among the three estuaries, the catch curves generally provided a poor fit to the data. The poor relationship most likely results from variability in recruitment patterns and the persistence of a few strong year classes, and highlights the sensitivity of catch-curve analysis to violations of the underlying assumptions of constant recruitment and constant mortality among cohorts. Variability in recruitment biases estimates of mortality using catch curves (Ricker 1975). The variable year-class strength observed for all sites suggests that recruitment may not be constant for eastern coast populations of *P. macrochir*. Halliday *et al.* (2008) reported a positive association between year-class strength and the timing and duration of freshwater flow events for *P. macrochir* in the Fitzroy River, with high flow events in spring and summer leading to increased survivorship. Such variability in recruitment may be responsible for the few strong year-classes and subsequent poor correlations of the catch curves observed here.

Reproductive biology

On the basis of elevated GSIs and the presence of mature and spawning fish, it was concluded that *P. macrochir* spawns between October and March at each site on the eastern coast of Queensland, with peak spawning occurring between October and December. This result is generally consistent with *P. macrochir* populations in northern Queensland (Russell 1988), and along the Pilbara and Kimberly coasts of Western Australia (Pember *et al.* 2005). In contrast, spawning of *P. macrochir* in the Gulf of Carpentaria in Queensland is reported to occur between late austral winter and early spring (McPherson 1997). The observed protracted spawning season suggests that eastern coast populations of *P. macrochir* may display indeterminate fecundity, with each mature individual capable of spawning on multiple occasions, as has been documented for *P. macrochir* in Western Australia (Pember *et al.* 2005).

A positive association between growth and maturity and sex-change schedules was observed among the three sites, in that fish from the Fitzroy River generally grew larger, and matured and changed sex at greater lengths and ages than those from the Mary or Brisbane Rivers. The timing of maturity and sex change appears to be highly flexible, as indicated by the large overlap in the length and age of immature and mature individuals and males and females, respectively. Such an overlap indicates that these processes may be phenotypically plastic and under social and/or hormonal control, with males being able to mature or change to females in response to local conditions, rather than at a predetermined length or age. Social control of sex change has been documented for several hermaphroditic species (Robertson 1972; Munday *et al.* 2006; Rodgers *et al.* 2007). The positive association of growth and maturity and sex-change schedules suggests that size plays an important role in the timing of maturity and sex change in the eastern coast populations of *P. macrochir*. For species in which sex change is under social control, the size-advantage hypothesis (Ghiselin 1969; Warner 1975) predicts that sex change will occur when individuals experience higher reproductive success as one sex when small or young and a greater reproductive success as the opposite sex when large or old. By assessing the size-advantage hypothesis with respect to reproductive value, an individual is predicted to change sex on the basis of its reproductive value as a male or female, relative to the size and sex composition of other individuals in a mating population (Warner 1988; Munday *et al*. 2006). Additionally, exogenous factors, such as population density and fishing pressure, also affect the timing of sex change in hermaphroditic species (Law 2000; Platten *et al*. 2002; Munday *et al*. 2006; McCormick *et al*. 2010). Platten *et al*. (2002) observed a negative relationship between mortality and age of sex change for the protogynous *Choerodon venustus*, with populations with higher mortality rates changing sex at smaller sizes and younger ages. Such factors may play a role in the spatial variation in length and age of sex change observed here.

Implications for management

The results of the present study highlight the importance of gaining an understanding of the spatial patterns in demography of exploited fish populations. The significant spatial variation in demography suggests that spatially separated populations of *P. macrochir* are likely to respond differently to fishing pressure and may therefore require spatially distinct management arrangements (Begg *et al*. 2005; Mapstone *et al*. 2008). Failure to take account of such differences in stock assessments and subsequent management arrangements may lead to less productive populations being over-fished, whereas potential yields may not be realised for more productive components (Williams *et al*. 2006). The spatial differences in demography of *P. macrochir* should ideally be incorporated into fisheries assessment models for this species, to obtain reliable model outputs and to optimise management.

Polydactylus macrochir is currently not subject to monitoring in Queensland waters. Given its apparent over-exploitation elsewhere in Australia (Pember *et al*. 2005; Moore *et al*. 2010), a proactive approach to management is strongly recommended to ensure sustainability of eastern coast populations of *P. macrochir*. Spatially distinct landings and demography should be monitored closely for signs of over-exploitation, including truncation of length and age classes and changes to length-at-age, maturity and sex-change profiles.

The minimum legal length (MLL) of 60-cm TL (49-cm FL) is well below the length at 50% maturity observed for each of the three sites. Our finding that 50% of the *P. macrochir* population matures at a larger size than the current MLL suggests that this regulation is inappropriate if the goal of the current fishery management practices is to allow the majority of male fish to spawn at least once before they can legally be retained. If the goal of the MLL is to allow at least 50% of males to spawn at least once, then the MLL should be increased at all sites. The effectiveness of increasing the MLL, however, relies on a high survival rate of released fish. Although the survival rates of net-caught *P. macrochir* individuals are undetermined, anecdotal evidence suggests that they are generally poor and negatively correlated with time spent in the net (B. Moore, pers. obs.). As such, increases to the MLL may be counter-productive, with a significant proportion of the captured *P. macrochir* individuals being required to be returned to the water in a moribund state.

Potentially, a more effective management strategy to ensure sustainability of *P. macrochir* populations may be to introduce a maximum legal length to protect females. Unlike barramundi, which has a maximum legal size of 1200-mm TL, there is no maximum legal size for *P. macrochir*. Given the large size at which *P. macrochir* changes sex, the minimum legal size limit of 600-mm TL does not afford effective protection of the female spawning stock. Because fisheries for protandrous species such as *P. macrochir* have a greater effect on the spawning biomass of females, owing to the tendency for fishing to selectively remove larger, older individuals of a population (Milton *et al*. 1998, 2005; Blaber *et al*. 1999), the potential exists for fishing activities to lead to biological alteration, egg limitation and overall reduced reproductive success (Blaber *et al*. 1996, 1999; Friedlander and Ziemann 2003). Owing to its rarity, female *P. macrochir* is disproportionately important to the reproductive success of a population. While our results suggest that *P. macrochir* recruits to the fishery at each site at 4 years old, 50% of individuals do not change sex until they are between 7 and 10 years old, depending on the site. As such, most fish are subjected to 3–6 years of fishing pressure before they can contribute to the population as females. Introduction of a maximum legal length may offer some protection for the larger females, thus potentially preventing egg limitation and recruitment overfishing. As with increases to the MLL, the effectiveness of a maximum legal length relies on a high survival rate of released fish. Further research into the survivorship of net-caught fish is warranted to fully understand the effectiveness of size limits as a management tool for eastern coast populations of *P. macrochir*. A reduction in the maximum net mesh diameter may be a viable alternative in reducing the fishing pressure on female *P. macrochir*, and warrants further research.

Estuarine fishes are particularly vulnerable to anthropogenic influences because of their proximity to human populations, where fishing pressure and habitat degradation are typically high. Fishing is one of the major anthropogenic factors affecting estuarine waters, and has been implicated in the decline and/or collapse of some coastal ecosystems (Pauly *et al*. 1998; Jackson *et al*. 2001). Given such pressures, it becomes increasingly important to obtain clearer insight into the spatial patterns in demography of exploited estuarine fishes. Demographic estimates derived for spatially distinct local populations, such as those observed in the present study, are likely to significantly improve stock assessments and advice for the management of particular species and their stocks.

Acknowledgements

Funding for this project was provided in part by the Fisheries Research and Development Corporation (Project no. 2007/032). Michelle Sellin and Ian Halliday (Department of Employment, Economic Development and Innovation, Queensland) kindly provided access to their image analysis system, otolith reference collection and assistance in otolith annuli interpretation. We are greatly indebted to the commercial fishers and fish processors who kindly supplied samples and allowed research staff on-board their vessels, and to the recreational fishers who retained samples, in particular Paul

Graveson, Ray Kennedy, Darryl Lund, Andrew Olds and Dan Watters who provided multiple samples. Aaron Ballagh provided assistance in collecting and processing some of the Fitzroy River samples, and John Page assisted with the fishery-independent sampling in the Brisbane River. Sampling in the Brisbane River was carried out under QDPI&F General Fisheries Permit no. 123692 to BRM and animal ethics project number A1214/06 (Animal Ethics Committee, James Cook University). Malcolm Haddon (CSIRO) provided advice on the likelihood-ratio test. BRM was supported in part by an Australian Postgraduate Award. We thank Bob Lester and Tom Cribb (University of Queensland) and two anonymous reviewers for their helpful comments on an earlier draft of the manuscript.

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Manuscript received 11 February 2011, accepted 23 April 2011