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***Highlights**

Highlights:

We examined life history traits to provide preliminary data on connectivity of *P. macrochir*. Samples from 18 locations across northern Australia were examined. Significant variation in growth, mortality and length-at sex change was observed among locations. Variation suggests likely presence of spatially discrete groups of at least post-recruitment fish.

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Spatial variation in life history reveals insight into connectivity and geographic population structure of a tropical estuarine teleost: king threadfin, *Polydactylus macrochir*

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Running headline: Spatial patterns in life history of *Polydactylus macrochir*

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Abstract

Understanding the life history of exploited fish species is not only critical in developing stock assessments and productivity models, but has a dual function in the delineation of connectivity and geographical population structure. In this study, patterns in growth, mortality, and length and age at sex change of *Polydactylus macrochir*, an ecologically and economically important protandrous estuarine teleost, were examined to provide preliminary information on the species' connectivity and geographic structure across northern Australia. Considerable variation in life history parameters was observed among the 18 locations sampled. Both unconstrained and constrained (t_0=0) estimates of von Bertalanffy growth function parameters differed significantly among all neighboring locations with the exception of two locations in Queensland's east coast and two in Queensland's Gulf of Carpentaria waters, respectively. Comparisons of back-calculated length-at-age 2 provided additional evidence for growth differences among some locations but were not significantly different among locations in the south-eastern Gulf of Carpentaria or on Queensland's east coast. Total mortality rates varied among locations, and were highest for estuaries within the Gulf of Carpentaria. The length and age at sex change differed markedly among locations, with fish from the east coast of Australia changing sex from males to females at significantly greater lengths and ages than elsewhere. Sex change occurred earliest at locations within Queensland's Gulf of Carpentaria, where a large proportion of small, young females were recorded. The observed differences suggest that *P. macrochir* likely form a number of geographically and/or reproductively distinct groups in Australian waters and suggest that future studies examining connectivity and geographic population structure of estuarine fishes will likely benefit from the inclusion of comparisons of life history parameters.

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Keywords: Life history; Movement; Stock structure; Fisheries management; Polynemidae, Australia

1. Introduction

Understanding the degree of exchange between geographically isolated groups of a species, or connectivity, is fundamental to the effective management of marine organisms (Begg et al., 1999a; Thorrold et al., 2001). Connectivity, which may occur through the movement of all life history stages (Gillanders, 2009), influences the distribution and abundance of organisms, rates of local adaption and speciation, the dynamics and persistence of populations, and the ability of ecosystems and species to recover from disturbance (Cowen et al., 2000; Slatkin, 1987). As such an understanding of connectivity is vital for determining the appropriate spatial scale at which a species should be managed (Begg et al. 1999a; Fogarty and Botsford, 2007). For exploited species, the application of management measures that fail to accurately define the degree of exchange or opportunity for replenishment to local populations may lead to over-fishing, resulting in dramatic changes in the biological attributes and productivity rates of a species, as well as changes in genetic diversity (Dominguez-Petit et al., 2008; Ricker, 1981; Smith et al., 1991), and localised depletion or extinction (Clark et al., 2000; Hilborn and Walters, 1992; Hutchings, 1996). Despite such critical importance, patterns of movement and connectivity are poorly understood for many species, particularly in tropical systems (Gillanders, 2009; Jones, 2006; Secor and Rooker, 2005).

In addition to being critical components in the development of stock assessments and productivity models, life history parameters, such as age and growth relationships, mortality rates, reproductive profiles, fecundity, distribution and abundance, have been used to provide preliminary data on the connectivity and geographic structure of fish populations (Abaunza et al., 2008; Begg et al., 1999b; Jennings and Beverton, 1991; Silva et al., 2008). The principle of the technique is that where the life histories of fish are the same, the fish either have grown in a similar environment or have a common history. Where different, it suggests that fish have spent at least part of the lives growing under different conditions and therefore may be geographically and/or reproductively isolated (Begg, 2005; Caselle et al., 2011; Ihssen et al., 1981). Patterns of growth, reproductive schedules and mortality rates also provide important data for biological monitoring, and may provide an indication of a species or population's vulnerability to over-exploitation (Haddon, 2001; Ricker, 1975).

To date, the application of life history parameters as a tool to delineate fish geographic population structure has largely focused on pelagic or groundfish species (Abaunza et al., 2008; Begg et al., 1999b; Silva et al., 2008). Although a number of studies have explored spatial patterns in life histories of estuarine fishes (Bedee et al., 2002; Gray et al., 2010; Robins et al., 2006; Sarre and Potter, 2000), few studies have examined life history parameters in the context of delineating connectivity and geographic population structure in these environments. As a growing body of evidence suggests that the biology of estuarine fish is strongly linked to the environment in which they reside (Halliday et al., 2008; Robins et al., 2006; Staunton-Smith et al., 2004), spatially isolated groups of estuarine fishes would be expected to exhibit significantly different life history parameters, particularly where differences in environmental conditions between locations are pronounced.

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The king threadfin, *Polydactylus macrochir* Günther, 1867 is a large, protandrous polynemid endemic to tropical and sub-tropical estuaries and turbid coastal waters across northern Australia, southern Papua New Guinea and Irian Jaya (Motomura et al., 2000). In Australia, the species' distribution extends from the Ashburton River in Western Australia across northern Australia to Brisbane in southeast Queensland (Motomura et al., 2000). *P. macrochir* has a life span of at least 22 years and an estimated maximum attainable size of approximately 40 kg and 170 cm fork length (Kailola et al., 1993; Moore et al., 2011), and is an important component of estuarine ecosystems, with dietary studies showing the species is a significant predator of crustaceans and small fishes (Brewer et al., 1995; Salini et al., 1998). The species supports valuable commercial, recreational and indigenous fisheries across northern Australia and form the second most important target species for northern Australia's inshore net fisheries after the barramundi, *Lates calcarifer* Bloch, with a reported 883 tonnes harvested commercially across Australia in 2008. The species is also targeted by recreational anglers throughout its distribution, and is highly regarded as both a table and sport fish (Kailola et al., 1993). However, despite its ecological and economic importance, little is currently known on the movements of the species. Knowledge of movement and connectivity between *P. macrochir* populations is therefore considered critical to ensuring sustainable management of the species.

In a preliminary study, Moore et al., (2011) observed significant variation in life history of *P. macrochir* among three estuaries spanning approximately 700 km on the east coast of Queensland. In this study, patterns in life history of *P. macrochir* are examined across the species' greater Australian distribution, as part of a multidisciplinary approach to determining connectivity of *P. macrochir* in Australian waters. Specifically, spatial patterns in age, growth, mortality rates and length and age at sex change are examined. It

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was hypothesised that as an estuarine species with a typically fragmented distribution, *P. macrochir* would show limited movement and exchange among locations that would manifest as differences in life history parameters.

2. Material and methods

2.1 Sample collection

P. macrochir were collected from 18 locations (estuarine stretches of rivers and coastal sites) across northern Australia between July 2007 and March 2010 (Fig. 1). Samples from the Fitzroy, Mary and Brisbane Rivers, analysed by Moore et al. (2011), were included in the present study to allow for comparison of these locations against those across northern Australia. At each location (with the exception of the Brisbane River and Lucinda), whole fish or fish frames (whole skeleton remaining after filleting) were obtained directly from commercial fishers, fish processors or by fisheries-independent sampling that generally used the same gear used by commercial fishers (i.e. a combination of gillnets of 100 mm (4 in.) to 165 mm (6.5 in.) stretched mesh). Brisbane River samples were collected through a fishery-independent sampling program using gillnets of 150 mm (6 in.) to 165 mm (6.5 in.) stretched mesh (n = 34), by opportunistic collections from recreational fishers (n = 42), and by research line-fishing (n = 9), whereas Lucinda samples were obtained from recreational fishers. For each fish collected, total length (TL), length to caudal fork (FL) and upper jaw length (UJL) were measured to the nearest millimetre unless damaged. Sex and maturity stage was determined from a macroscopic examination of the gonads, based on the criteria of Pember et al. (2005) and Moore et al. (2011). As some samples were eviscerated at sea it was not possible to determine sex and maturity stage for all specimens. Sagittal otoliths (hereafter referred to as otoliths) were removed for

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all specimens, cleaned, dried and stored in paper envelopes until processing in the laboratory. Although fishery regulations for this species is based on TL, we have generally analysed and presented FL data, as the fishery-sourced samples frequently had damage to the distal margins of the tail, precluding accurate TL measurements for some specimens. Total lengths were estimated using the equation of Moore et al. (2011), where TL = 1.1737FL + 22.083 ($r^2 = 0.99$, $n = 635$).

2.2 Age determination

Ages of *P. macrochir* were estimated from whole and sectioned otoliths, following the procedure outlined in Moore et al. (2011). Briefly, otoliths in which six or fewer annuli were counted in an initial whole read were read whole again, whereas otoliths in which more than six annuli were counted in the initial read were sectioned. Once the method of reading was established, each otolith was read twice. When annuli counts between the two reads did not agree, a third reading was taken, and the two concurrent readings being accepted as the number of annuli. When all three counts differed, the otolith was rejected from further analysis. All otoliths were interpreted by a single reader (BRM) to ensure consistency.

The age of each fish was estimated from the number of annuli, the assumed birth date, the estimated date of annuli deposition, and the date of capture. Birth dates were estimated from the middle of the peak spawning period for each major water body. A birth date of 1 November was assumed for *P. macrochir* collected from the northwest coast of Western Australia (Pember et al., 2005) and Queensland’s east coast (Moore et al., 2011), whereas a birth date of the 1 September was assumed for fish collected from the Gulf of Carpentaria (McPherson, 1997). Although little is known about the timing of spawning of *P. macrochir*

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along the northern coast of the Northern Territory, a birth date of 1 November was assumed in these waters, consistent with observations of peak spawning reported by fishers (Ian Halliday, pers. comm.). A common date of annuli completion of 31 October was assumed for fish from all locations, years and age classes, consistent with Moore et al. (2011) and Pember et al. (2005). There was no evidence to suggest that Gulf of Carpentaria populations laid down a visible opaque zone in their first October of life (i.e. when they were 1 month old). The ageing algorithm took the form:

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

where age_{m} is the age in months, n is the number of annuli, m_{b} is the number of months for the assigned birth date to the date of annuli completion, 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 sex change. Year classes were assigned on the basis of the peak spawning period (i.e. fish from the Fitzroy River spawned between October 2005 and January 2006 are from the 2005 year class).

2.3 Data analysis

2.3.1 Growth comparisons

Growth was compared among locations using two methods. In the first method, the von Bertalanffy growth function (VBGF) was fitted by nonlinear least-squares regression of FL on yearly fractional age of *P. macrochir*. The form of the VBGF used to model length-at-age data was:

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

where L_t is the length mean of fish at age t, 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. To examine the effect of the low numbers of fish <2 years in the samples a second set of analyses was conducted on data with the t_0 constrained to zero. Unconstrained and constrained VBGFs were compared among locations using likelihood ratio tests. A common range of ages was used in the analyses to ensure validity of the comparisons (Haddon, 2001).

Due to the lack of older individuals in some of the samples, biologically meaningful comparisons of VBGF parameters could not be conducted for all locations. As such, a second analysis of growth, based on comparisons of back-calculated FL at age 2, was conducted. To establish the relationship between FL and otolith radius at the time of capture (OR), the distance from the nucleus of the otolith to its periphery was measured in 1,430 randomly selected individuals covering a range of ages and locations using the Image ProPlus image analysis system. Measurements were always taken at the furthest point of the structure (Fig. 2). The relationship between OR at time of capture and FL was then determined by ordinary least-squares regression. Between-location differences in the FL-OR relationship could not be examined at all locations due to the unreliability of the small sample sizes at some locations. However, ANCOVA revealed no significant difference in the relationship among 11 locations covering the geographical distribution of the sampling program, that all had relatively large sample sizes ($F_{10,1032} = 1.68$, $P = 0.08$). Combined with the propinquity of the data points from the overall regression (Fig. 3) this suggests that any between-location differences in the fork length to otolith radius were

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negligible. Thus, data were pooled across locations to establish the relationship between fork length and otolith radius.

To establish the back-calculated length-at-age 2, a second measurement from the otolith nucleus to the furthest point of the second annulus was taken for each fish from the 2005 year class (Fig. 2). The 2005 year class was selected to reduce the effect of temporal variation in growth, as it was common to most locations. Back-calculated length-at-age 2 was then determined by substituting this measurement into a body proportional equation (Francis, 1990). The length of an individual fish when the second band was laid down (FL_2) was calculated as:

$$FL_2 = (R_2/OR)^{v}FL$$

where R_2 is the distance from the otolith nucleus to the furthest point of the second annuli, FL is the fork length at capture and v is the constant derived from the power function that best described the relationship between FL and OR. The power function took the form $FL = 23.271 \times OR^{1.463}$, $R^2 = 0.864$, $P < 0.0001$ (Fig. 3). Shapiro-Wilk tests revealed that the derived length-at-age 2 data were non-normally distributed ($P < 0.05$), so to satisfy assumptions of normality and homogeneity of variances the data were log-transformed prior to analysis. One-way analysis of variance (ANOVA) was used to test for differences in back-calculated lengths-at-age 2 among locations using location as a fixed factor. Significant results were examined using Tukey-Kramer post-hoc pairwise comparisons. Only locations that had at least 10 individuals were considered in the analysis, which is similar to the samples sizes used by Abaunza et al. (2008) and Erzini (1994) in their respective studies of variability of length-at-age of marine fishes.

2.3.2 Mortality

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Total instantaneous mortality rates (Z) were estimated 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. Total mortality was estimated as the absolute value of the regression slope, b. Regressions were fitted from the modal age class, presumed to be the first age class fully selected by the sampling gear, through to the oldest age class that was preceded by no more than two zero frequencies. Estimates of Z were compared among locations by analysis of covariance (ANCOVA), with age as the covariate. Due to low sample sizes and a general lack of older individuals for some locations, mortality rates were calculated only for those locations where comparisons of VBGF parameters were conducted.

2.3.3 Length and Age at Sex Change

The length and age at which 50% of *P. macrochir* changed sex at each of the locations was determined by logistic regression analysis, using the equation:

$$Ps = 1/[1 + \exp(-\ln(19)\,(s - s_{50})/(s_{95} - s_{50}))]$$

where Ps = the proportion of females in each 50 mm length or age class s, $s50$ and s95 are the ages or lengths at which 50% and 95% of the population have changed to females, respectively. Due to low numbers, transitional individuals were excluded from the analysis. The data (male or female) for individual fish were randomly re-sampled 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. Approximate 95% confidence limits of the parameters were calculated as the 2.5 and 97.5 percentiles of the parameter estimates obtained from the re-sampling technique. The point estimates for each parameter and of the probability of fish being female at each specified length or age were taken as the medians of the bootstrap estimates. Following Moore et al. (2011), non-overlapping confidence intervals were used to indicate significant differences in sex change profiles among locations.

3. Results

3.1 Growth comparisons

Considerable differences were observed in the maximum age of *P. macrochir* between locations. Fish aged eight years or older were recorded at only 10 of the 18 locations sampled (Table 1). The oldest fish (21.9 years) was recorded from the Fitzroy River, whereas the maximum age of fish from locations in Western Australia and the Queensland's Gulf of Carpentaria was 11.5 and 8.5 years, respectively.

Due to the lack of older individuals at some locations, estimation and comparison of the VBGF parameters were considered appropriate for only the 10 locations that contained fish that were eight years of age or older. In general, the constrained fit of the VBGF typically resulted in slightly lower estimates of L_∞ and slightly higher estimates of K than the unconstrained fit (with the exception of samples from Derby, the Flinders River, Spring Creek and the Mary River) (Table 2). Differences between the constrained and unconstrained fits, however, were generally minimal (Fig. 4), suggesting that a sufficiently wide range of length and age classes were sampled to establish biologically reasonable estimates of growth without the need to constrain t_0.

Both constrained and unconstrained VBGF parameters estimates showed considerable difference among locations. Likelihood ratio tests of unconstrained VBGFs of fish across common age classes indicated that growth differed amongst all locations at $P = 0.05$, with the exception of Derby and the Mary River ($\chi^2 = 6.576$, $P = 0.087$), the Flinders River and Spring Creek ($\chi^2 = 5.211$, $P = 0.157$) and the Mary and Brisbane Rivers ($\chi^2 = 6.191$, $P = 0.103$). Likelihood ratio tests of constrained VBGFs confirmed the similarity observed in the comparisons of the unconstrained growth estimates of fish from the Flinders River and Spring Creek ($\chi^2 = 6.679$, $P = 0.083$) and the Mary and Brisbane Rivers ($\chi^2 = 0.759$, $P = 0.684$). All other comparisons, with the exception of Eighty Mile Beach and Spring Creek ($\chi^2 = 1.366$, $P = 0.505$), Roebuck Bay and Chambers Bay ($\chi^2 = 5.289$, $P = 0.071$), and the Roper River and Fitzroy River ($\chi^2 = 5.227$, $P = 0.073$) were significantly different at $P = 0.05$.

One-way ANOVA revealed that the back-calculated lengths-at-age 2 differed significantly among sites ($F_{16,389} = 18.6$, $P < 0.01$). Tukey-Kramer pair-wise comparisons gave an indication of the similarity among the spatially distinct samples (Table 3). Samples from Eighty Mile Beach and Roebuck Bay differed significantly, with Roebuck Bay samples generally being larger than those from Eighty Mile Beach (Fig. 5). Samples from Derby differed to those of neighbouring Roebuck Bay and Chambers Bay. No difference was observed among Chambers Bay, Roper River, Kendall River or Wenlock River samples. Samples from Arthurs Creek, the Albert and Flinders Rivers, Morning Inlet, and Spring Creek in Queensland's south-eastern Gulf of Carpentaria waters were not significantly different, suggesting that these fish had either grown in a similar environment or moved between locations. Samples from these locations were generally smaller than those from all other Gulf of Carpentaria locations (Fig. 5). No significant difference was observed among the five locations on the east coast of Queensland (Lucinda, Townsville, and the Fitzroy, Mary and Brisbane Rivers).

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3.2 *Total mortality*

Total mortality (*Z*) estimates differed significantly among the ten locations where comparisons were possible (ANCOVA, $F_{9,81} = 3.97$, $P < 0.001$) (Table 2). Locations in the Gulf of Carpentaria (Flinders River, Spring Creek and the Roper River) had the highest estimates of *Z*, whereas *Z* was lowest for the Fitzroy River, Chambers Bay and Eighty Mile Beach.

3.3 *Length and age at sex change*

In general, there was a large overlap in the length distributions of males and females (Fig. 6). Males typically dominated the smaller length classes and females dominated the larger length classes for samples from Eighty Mile Beach, Roebuck Bay, Derby, Chambers Bay, and the Roper, Fitzroy, Mary and Brisbane Rivers. In contrast, there were a large proportion of small, young females from the seven locations in the south-east Gulf of Carpentaria (Arthurs Creek, Albert River, Morning Inlet, Flinders River, Spring Creek, and the Kendall River) (Fig. 6). A general lack of increase in the proportion of females with both length and age was observed at these locations, precluding any estimates of the length and age at which 50% of the population changed sex, even when data for these locations were pooled. The general absence of young females at sites outside of the Gulf of Carpentaria (Fig. 6) suggests little movement, at least of female fish, to these locations from those within the Gulf.

Due to low numbers of females at some locations and the lack of increase in proportion of females with length or age for locations in the south-east Gulf of Carpentaria, estimates of the length and age at which 50% of the population changed sex were possible for only seven of the 18 locations sampled (Fig. 6; Table 4). Considerable variation was

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observed in both the length and age at sex change among the seven locations (Table 4). The estimated length at which 50% of the population was female (i.e. L_{50}) was lowest for Eighty Mile Beach (450 mm FL) and highest for the Fitzroy River (1140 mm FL) (Table 4). The L_{50} of fish from Eighty Mile Beach, Chambers Bay and the Fitzroy River each appeared significantly different to all other locations. No significant differences in the L_{50} estimates were observed among Roebuck Bay and Derby, or the Mary and Brisbane Rivers (Table 4). The estimated age at which 50% of the population was female (i.e. A_{50}) was lowest for Eighty Mile Beach (2.0 years) and highest for the Fitzroy River (9.7 years) (Table 4). The A_{50} of fish from Eighty Mile Beach was significantly lower than all other locations. Overlapping confidence intervals indicated no significant differences in the A_{50} estimates among Roebuck Bay and Derby, the Fitzroy, Mary and Brisbane Rivers, and Chambers Bay and the Mary and Brisbane Rivers (Table 4). All other comparisons were significantly different, as indicated by non-overlapping 95% confidence intervals.

4. Discussion

The use of life history parameters to provide information on the connectivity and geographic population structure of fishes relies on differences in one or more biological parameter between locations (Begg et al., 1999b). In the present study, significant variation was observed in growth patterns, rates of total mortality and length- and/or age-at-sex change profiles of post-recruitment assemblages of *P. macrochir*, at a range of spatial scales in Australian waters. Differences in life history parameters over similar spatial scales as those observed here have been reported for several estuarine species, including black bream, *Acanthopagrus butcheri* (Sarre and Potter, 2000), spotted sea trout, *Cynoscion nebulosus* (Bedee et al., 2002) and luderick, *Girella tricuspidata* (Gray et al., 2010).

A key limitation of using life history data to comment on connectivity of fishes is that the technique seldom provides information the genetic relationships amongst groups. Although potentially mediated by both genetic and environmental factors, life history parameters are frequently predominantly characterised by the environment or exploitation rates a fish experiences over its life history, because of their sensitivity to extrinsic variables (Beacham 1982, Begg, 2005). Accordingly, the approach provides little information on dispersal and connectivity of egg and larval life history stages. In the case of *P. macrochir*, it may be that recruits originate from a single common source, or number of common sources, that export individuals to locations with different environmental conditions or exploitation rates which ultimately generate the different life history patterns observed. While this possibility cannot be ruled out from the life history data, the observed spatial differences in life history parameters suggests limited movement and connectivity of at least post-recruitment fish, which in itself has important implications for management. If there was broadscale mixing of post-recruitment fish among locations, the life histories amongst locations would be similar (Begg et al., 1999b; Ihssen et al., 1981).

The spatial structure of post-recruitment *P. macrochir* evident from the life history data is generally consistent with concurrent research into the movements and stock structure of the species, suggesting comparisons of life history data may provide a reliable method of identifying spatially-discrete adult assemblages of *P. macrochir*. For example, the similarities observed in growth and length and age at sex change for *P. macrochir* in the south-eastern Gulf of Carpentaria, is in accordance with recent investigations of mitochondrial DNA haplotypes (Horne et al., in review) and whole otolith oxygen ($\delta^{18}O$)

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and carbon ($\delta^{13}C$) stable isotope ratios (Newman et al., 2010), which suggests the occurrence of a single demographic population in this region, with extensive mixing of post-recruitment stages of *P. macrochir*. Nevertheless, some discrepancies are evident between these complementary techniques. Newman et al. (2010) found no difference in otolith stable isotope ratios of fish from Eighty Mile Beach and Roebuck Bay, whereas significant variation was observed in VBGF parameters, back-calculated lengths-at age 2 and length and age at sex change among these locations in the present study, suggesting fish from these locations may form spatially discrete groups, or stocks. These apparently conflicting results among methodologies highlight the importance and value in using multiple techniques to determine the movement and connectivity of fishes. Begg et al. (1999b) consider that life history parameters should be used as a preliminary technique to identifying stock structure of fishes, before applying more refined methods, such as analyses of parasite assemblages or otolith elemental signatures. Such an approach may further corroborate and refine the spatial patterns observed here.

It is unclear what effect temporal differences in life history parameters had on the spatial comparisons. Numerous studies have documented temporal variation in life history parameters that have occurred in response to changing environmental conditions and/or exploitation patterns (e.g. Begg et al., 1999b; DeVries and Grimes, 1997). In the present study, it was necessary to pool location-specific collections within or among years due to small sample sizes, which may have potentially confounded spatial patterns between locations. However, comparisons of growth of Fitzroy River fish caught between 2007 and 2009 revealed that while growth varied from year to year, these differences were of a much reduced magnitude compared with those observed between the Fitzroy River and other locations (B. Moore, unpublished data).

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As locations were generally sampled with similar gear (i.e. a combination of gillnets of 100 mm (4 in.) to 165 mm (6.5 in.) stretched mesh at each location), it is unlikely that the differences in life history parameters reflect differences in sampling methods among locations. Although samples from Lucinda and some Brisbane River fish were collected from recreational fishers, it is unlikely that these differences in sampling gear confounded comparisons with net-caught fish, as Moore et al. (2011) found no significant differences in length-at-age between gillnet- and recreationally-caught samples from the Brisbane River, suggesting negligible effects of any size-selectivity between netting and recreational fishing methods in this case. Furthermore, although the sample sizes varied markedly among locations, it is unlikely that these differences affected the comparisons of VBGF parameters, because these analyses were conducted on common age classes across the locations. Similarly, the unequal sample sizes are factored into the comparisons of back-calculated length-at-age and the development of the 95% confidence intervals for the comparisons of length and age at sex change, and thus are unlikely to confound these comparisons.

4.1 Causal mechanisms for the spatial patterns in life histories

A number of factors may be responsible for the differences observed in life history parameters of *P. macrochir*. In general, there was a positive association between longevity, growth and length- and age-at-sex change, suggesting that these parameters are strongly correlated. For example, fish from the Fitzroy River were generally found to live longer, obtain larger observed and hypothetical asymptotic lengths, and change sex at greater lengths and ages than elsewhere. The positive association of longevity, growth and sex change implies that size plays an important role in the timing of sex change in *P.*

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macrochir, a result that is consistent with the size advantage hypothesis of sex-allocation theory (Ghiselin, 1969; Warner, 1988).

It is unclear whether the spatial patterns reflect genetic differences between locations. Recent genetic examination of nine of the 18 locations examined in the present study (Eighty Mile Beach, Roebuck Bay, Chambers Bay, Albert River, Flinders River, Kendall River, Townsville, Fitzroy River and the Brisbane River), suggest that, with the exception of Eighty Mile Beach and Roebuck Bay, and the Albert, Kendall and Flinders Rivers, fish at each site constitute a genetically-discrete population (Horne et al., in review). Further fine-scale genetic examination, conducted across all locations examined here, is warranted to determine whether the spatial differences in life history parameters reflect genetic patterns.

Geographical differences in fishing pressure are also likely to play a significant role in the observed spatial patterns in life histories. Worldwide, fishing pressure has been demonstrated to cause significant biological change in fish populations, and has been implicated as the most likely cause of biological change in a variety of exploited species (e.g. Hidalgo et al., 2009; Millner and Whiting, 1996). Size-selective fishing gear such as gillnets may favor the survival of smaller individuals, leading to overall decreases in length-at-age (Ricker, 1981), or conversely may result in a reduction in population density, resulting in lower levels of competition and increased availability of food, leading to faster growth and an increase in length-at-age (Hidalgo et al., 2009; Millner and Whiting, 1996). In hermaphroditic species, the removal of larger, older individuals (typically those of the secondary sex) of a population through size-selective harvest practices has been documented to result in decreases in the length and age at sex change (Hawkins and Roberts, 2003; Platten et al., 2002). Such changes may have subsequent effects on growth

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rates, with individuals allocating energy to reproduction rather than to growth (de Roos et al., 2006).

Although it is difficult to elucidate the effect of fishing pressure from genetic and environmental factors, there is indirect evidence to suggest that fishing is an important causal mechanism of the observed spatial patterns in life histories. Populations on Queensland's east coast, and along the north coast of the Northern Territory, where fishing pressure has historically been light and total mortality was generally lowest, were found to live longer and change sex at greater lengths and ages than elsewhere. Conversely, populations in the south-eastern Gulf of Carpentaria, where fishing pressure has historically been the highest and total mortality was greatest, exhibited the smallest back-calculated lengths, youngest maximum ages and changed sex much earlier than at other locations. The lack of old fish, and the large proportion of small, young females observed at locations in Queensland's Gulf of Carpentaria waters relative to elsewhere across northern Australia, suggests *P. macrochir* may be over-fished in this region, and warrants further investigation.

Local environmental conditions, in particular freshwater flow, may also play an important role in the observed patterns in life history parameters (Davidson et al., 2010; Robins et al., 2006). Increases in freshwater flow has been suggested to affect growth of estuarine fishes via increased prey availability due to increases in nutrient availability and primary productivity (Robins et al., 2006; Whitfield, 2005), or by increased foraging opportunity under the protection of higher turbidities (Hecht and van der Lingen, 1992). Increases in freshwater flow have been documented to result in increased growth and trigger downstream movement of banana prawns *Penaeus merguiensis* (Vance et al., 1998; Vance et al., 1985), one of the dominant prey items for *P. macrochir* (Salini et al., 1998),

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which may make them more susceptible to predation. As such the spatial differences in life history parameters between locations may in part reflect differences in freshwater flow, however a general lack of flow data for most of the locations examined here precludes examination of the influence of freshwater flow on the observed spatial patterns in *P. macrochir* life histories.

In addition, factors such as temperature (Durieux et al., 2009; Tolan and Fisher, 2009), duration of spawning season (Choat et al., 2003; Robertson et al., 2005), parasite loadings (Adlard and Lester, 1994), or spatial differences in predator abundances or predation rates (Hixon, 1991; Hixon and Webster, 2002; Jones and McCormick, 2002) can also influence the life histories of fishes, and may have an influence here. It is likely that a combination of several of the above factors is responsible for the observed spatial patterns in life history parameters.

4.2 Implications and future directions

The life history parameters examined in this study have shown distinct spatial signatures, suggesting the probable existence of a number of spatially distinct groups of at least post-recruitment *P. macrochir* assemblages across northern Australia. This is in contrast to the current management arrangements for the species, whereby post-recruitment *P. macrochir* are managed as single, intermixing populations in the waters of Western Australia, the Northern Territory, Queensland's Gulf of Carpentaria and Queensland's east coast. While further techniques are required to accurately define the connectivity and structure of *P. macrochir* populations, the limited connectivity evident from the spatial differences in life history of post-recruitment *P. macrochir* suggests that management practices within each jurisdiction, such as the development of monitoring and assessment programs, harvest

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strategies and establishment of suitable fishery regulations, need to be reviewed to recognise the potential for localised depletion of adult *P. macrochir* assemblages. Furthermore, the observed variation in life history parameters within jurisdictional boundaries suggests that the spatially segregated populations of *P. macrochir* will likely respond differently to fishing pressure if managed as a single entity. 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 (Moore et al. 2011; Williams et al., 2006). The spatial differences in life history of *P. macrochir* should ideally be incorporated into fisheries assessment models for this species, to obtain reliable model outputs and to optimise management

Moore et al. (2011) suggest that the current minimum legal length of 60 cm TL in effect in Queensland waters is insufficient if its objective is to allow 50% of males the opportunity to spawn at least once before capture, however these authors cautioned that the success of increasing the minimum legal length is contingent on either a high survival rate of released fish, or fish not being selected for by the fishing gear. The fisheries-dependent collections examined by Moore et al. (2011), however, were largely sourced from fish processors, providing little information on the proportion of undersized fish captured by the commercial fleet. However, samples from the Gulf of Carpentaria examined in the present study were generally collected prior to an increase of the minimum legal size from 40 cm TL in these waters, or were collected by commercial fishers working under a Queensland fisheries collection permit. Thus, although the gear used reflects that used by the commercial fleet, these fishers were able to retain any fish smaller than the current minimum legal size that they collected, providing an indication of the proportion of the

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catch constituted by undersized fish that would normally be discarded. Of the 502 fish collected from Queensland's Gulf of Carpentaria, approximately 20% (115 individuals) were smaller than the current minimum legal size, indicating that undersized fish comprise a significant proportion of the catch in this region. Given that survival rates of net-caught *P. macrochir* are generally poor (B. Moore, pers. obs.), the majority of undersized fish would be returned to the water in a moribund state. As such, further increases in the minimum legal length, in isolation of other management measures, is likely to be ineffective in reducing fishing pressure on immature *P. macrochir*. An increase in the minimum net mesh size may be a viable alternative tool to reduce the fishing pressure on undersized individuals, and warrants further research.

The relative longevity and protandrous life history of *P. macrochir* makes the species particularly susceptible to overfishing. As fishing pressure is typically biased toward the larger, older individuals of a population, it is the females of protandrous species that are subjected to the greatest fishing mortality, which may lead to egg limitation and recruitment overfishing (Blaber et al., 1999; Milton et al., 1998). To help mitigate these effects on sex-changing species, fisheries managers commonly implement output controls such as maximum legal lengths or slot limits. There is currently no maximum legal length restriction for *P. macrochir* in any Australian waters. Introduction of a maximum legal length may offer some protection for the larger females. However, the effectiveness of a maximum legal length is contingent on fish surviving long enough to reach the proposed length, and on a high survival rate of released fish should fish over the maximum legal length be caught. Further research into the survivorship of net-caught fish is warranted to fully understand the effectiveness of size limits as a management tool for *P. macrochir*. A reduction in the maximum net mesh diameter may be a viable alternative in reducing the

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fishing pressure on female *P. macrochir*, by limiting the incidence of capture of these individuals.

This study has demonstrated the effectiveness of using life history parameters as a tool for assessing movement and connectivity of a large, tropical estuarine teleost, and suggests that future studies examining connectivity and geographical structure of estuarine fishes will likely benefit from the inclusion of comparisons of life history parameters. Holistic approaches that integrate multiple techniques have been advocated as the preferred approach to delineating patterns of movement, connectivity and stock structure of fishes (Begg and Waldman, 1999). Additional techniques, such as comparisons of parasite assemblages or otolith elemental signatures, used in synergy with the life history parameters analysed here, will likely shed additional light on the movements of *P. macrochir*, including connectivity of larval stages to post-recruitment assemblages, to provide a comprehensive understanding of patterns of movement and connectivity and the appropriate spatial scales for management, monitoring and assessment.

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Fig. 1. Locations where king threadfin, *Polydactylus macrochir*, were collected for examination of life history. Clockwise from left: EMB, Eighty Mile Beach; RB, Roebuck Bay; DBY, Derby; CB, Chambers Bay; RR, Roper River; AC, Arthurs Creek; AR, Albert River; MI, Morning Inlet; FLR, Flinders River; SC, Spring Creek; SR, Staaten River; KR, Kendall River; WLR, Wenlock River; LUC, Lucinda; TSV, Cleveland Bay, Townsville; FR, Fitzroy River; MR, Mary River; BR, Brisbane River.

Fig. 2. Sagittal otolith of a 3 year-old king threadfin *Polydactylus macrochir* from the Fitzroy River showing measurements made for back-calculation of length-at-age 2. OR is the radius of the otolith at capture and R_2 is the radius of the otolith at 2 years of age.

Fig. 3. Plot of fork length (mm) on otolith radius (mm) and the power relationship ($y = 23.271x^{1.463}$, $R^2 = 0.864$, $n = 1490$).

Fig. 4. Length at age data, unconstrained (solid lines) and constrained ($t_0 = 0$) (dashed lines) and von Bertalanffy growth function curves for *Polydactylus macrochir* in Australian waters. See Table 2 for parameter estimates.

Fig. 5. Back-calculated fork length-at-age 2 for *Polydactylus macrochir* from 17 locations across northern Australia. The mean, 25th and 75th percentiles (boxes) and 90th percentiles (whiskers) are represented in the boxplots. See Fig. 1. for location codes.

Fig. 6. Length frequency distributions for male (light grey) and female (dark grey) *Polydactylus macrochir* from 18 locations in Australian waters.

Fig. 6 (cont.). Length frequency distributions for male (light grey) and female (dark grey) *Polydactylus macrochir* from 18 locations in Australian waters.

Table 1

Summary of *Polydactylus macrochir* collected from 18 locations across Australia. Undetermined indicates fish that were eviscerated at sea.

Location	*n*	Mean age (years)	Age class range (years)	Mean FL (mm)	FL range (mm)	*n* males	*n* females	*n* transitionals	*n* undetermined
Eighty Mile Beach	150	4.9	1–12	687	228–1080	41	99	10	0
Roebuck Bay	319	2.8	1–10	635	451–919	260	55	4	0
Derby	61	4.0	1–10	698	210–1040	28	26	7	0
Chambers Bay	126	6.3	2–12	816	505–1030	73	52	1	0
Roper River	126	4.9	2–11	864	480–1090	20	6	1	99
Arthurs Creek	44	3.5	2–6	565	415–835	38	5	1	0
Albert River	36	3.7	3–5	599	520–715	31	5	0	0
Morning Inlet	54	3.6	2–7	567	325–1130	29	24	1	0
Flinders River	138	3.6	2–8	655	325–930	83	49	5	1
Spring Creek	103	3.5	2–9	611	295–1020	55	45	2	1
Staaten River	31	2.4	2–4	495	320–595	9	21	1	0
Kendall River	63	2.1	1–3	528	315–810	57	6	0	0
Wenlock River	33	2.7	2–5	679	442–960	29	3	0	1
Lucinda	25	3.6	3–4	801	645–895	18	0	4	3
Townsville	84	2.8	1–4	701	450–886	67	2	1	14
Fitzroy River	699	4.7	2–22	801	430–1354	241	29	6	423
Mary River	61	5.3	2–11	806	440–1016	47	8	1	5
Brisbane River	85	5.6	2–14	828	493–1062	58	18	2	7

Table 2

von Bertalanffy growth parameters and rates of total mortality for *Polydactylus macrochir* from ten locations across northern Australia.

Location	Unconstrained VBGF			Constrained ($t_0 = 0$) VBGF		Total mortality	
	L_∞ (mm)	K	t_o	L_∞ (mm)	K	Z	r^2
Eighty Mile Beach	1108	0.23	-0.26	1074	0.26	0.162	0.42
Roebuck Bay	888	0.46	-0.33	869	0.55	0.372	0.51
Derby	1176	0.26	0.10	1199	0.24	0.373	0.68
Chambers Bay	965	0.32	-1.05	942	0.46	0.120	0.20
Roper River	1094	0.33	-0.04	1091	0.34	0.626	0.89
Flinders River	835	0.53	0.53	1094	0.38	0.887	0.94
Spring Creek	978	0.35	0.48	1096	0.25	0.642	0.64
Fitzroy River	1222	0.24	-0.34	1201	0.27	0.119	0.49
Mary River	975	0.46	0.79	1018	0.33	0.311	0.46
Brisbane River	1047	0.30	-0.25	1034	0.33	0.298	0.55

Table 3

P-values from Tukey-Kramer pair-wise comparisons of back-calculated length-at-age 2 for king threadfin, *Polydactylus macrochir*, from the 2005 year class collected from 17 locations across northern Australia (bold indicates significant difference).

Location	RB	DBY	CB	RR	AC	AR	MI	FLR	SC	KR	WLR	LUC	TSV	FR	MR	BR
EMB	**<0.001**	0.459	**<0.001**	**<0.001**	0.518	0.072	1.000	0.509	**0.025**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.026**
RB		**<0.001**	1.000	0.056	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.000	0.652	0.998	0.194	**0.013**	0.972	**0.004**
DBY			**0.017**	**<0.001**	1.000	1.000	0.637	1.000	1.000	**0.012**	**<0.001**	0.209	0.419	0.668	0.528	1.000
CB				0.060	**<0.001**	**0.017**	**<0.001**	**<0.001**	**0.003**	1.000	0.541	1.000	0.899	0.513	1.000	0.098
RR					**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.161	1.000	**0.012**	**<0.001**	**<0.001**	**0.006**	**<0.001**
AC						1.000	0.740	1.000	0.999	**<0.001**	**<0.001**	**0.006**	**0.006**	**0.021**	0.061	0.990
AR							0.173	0.996	1.000	**0.012**	**<0.001**	0.271	0.509	0.782	0.660	1.000
MI								0.756	0.087	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.074
FLR									0.987	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.016**	0.943
SC										**0.002**	**<0.001**	0.127	0.223	0.482	0.485	1.000
KR											0.732	1.000	0.813	0.407	0.998	0.071
WLR												0.220	**0.005**	**<0.001**	0.130	**<0.001**
LUC													1.000	0.994	1.000	0.607
TSV														1.000	1.000	0.888
FR															1.000	0.984
MR																0.910

Table 4

Estimates of length and age (and upper and lower 95% confidence intervals) at which 50% of *Polydactylus macrochir* change sex at seven locations across northern Australia.

Location	Fork length (mm)			Age (years)		
	L_{50}	Lower 95% CI	Upper 95% CI	A_{50}	Lower 95% CI	Upper 95% CI
Eighty Mile Beach	450	308	541	2.0	0.2	3.3
Roebuck Bay	779	757	799	5.1	4.3	6.1
Derby	707	614	804	4.2	3.6	5.0
Chambers Bay	882	868	893	7.0	6.4	7.6
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

Figure 1

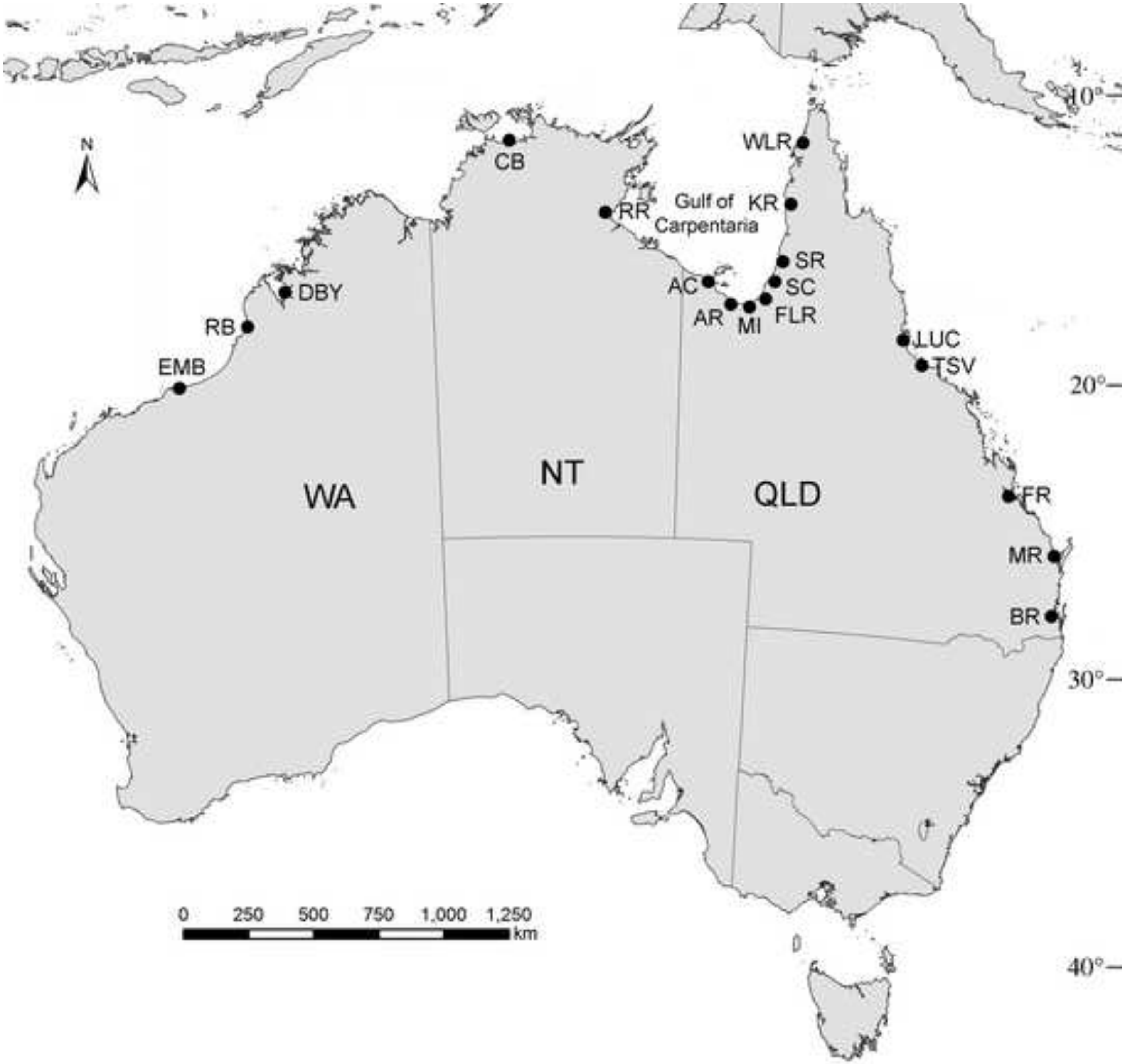

N
CB
WLR
Gulf of Carpentaria
KR
RR
SR
AC
SC
AR
MI
FLR
DBY
RB
EMB
LUC
TSV
WA
NT
QLD
FR
MR
BR
10°
20°
30°
40°
0
250
500
750
1,000
1,250
km

Figure 2
Click here to download high resolution image

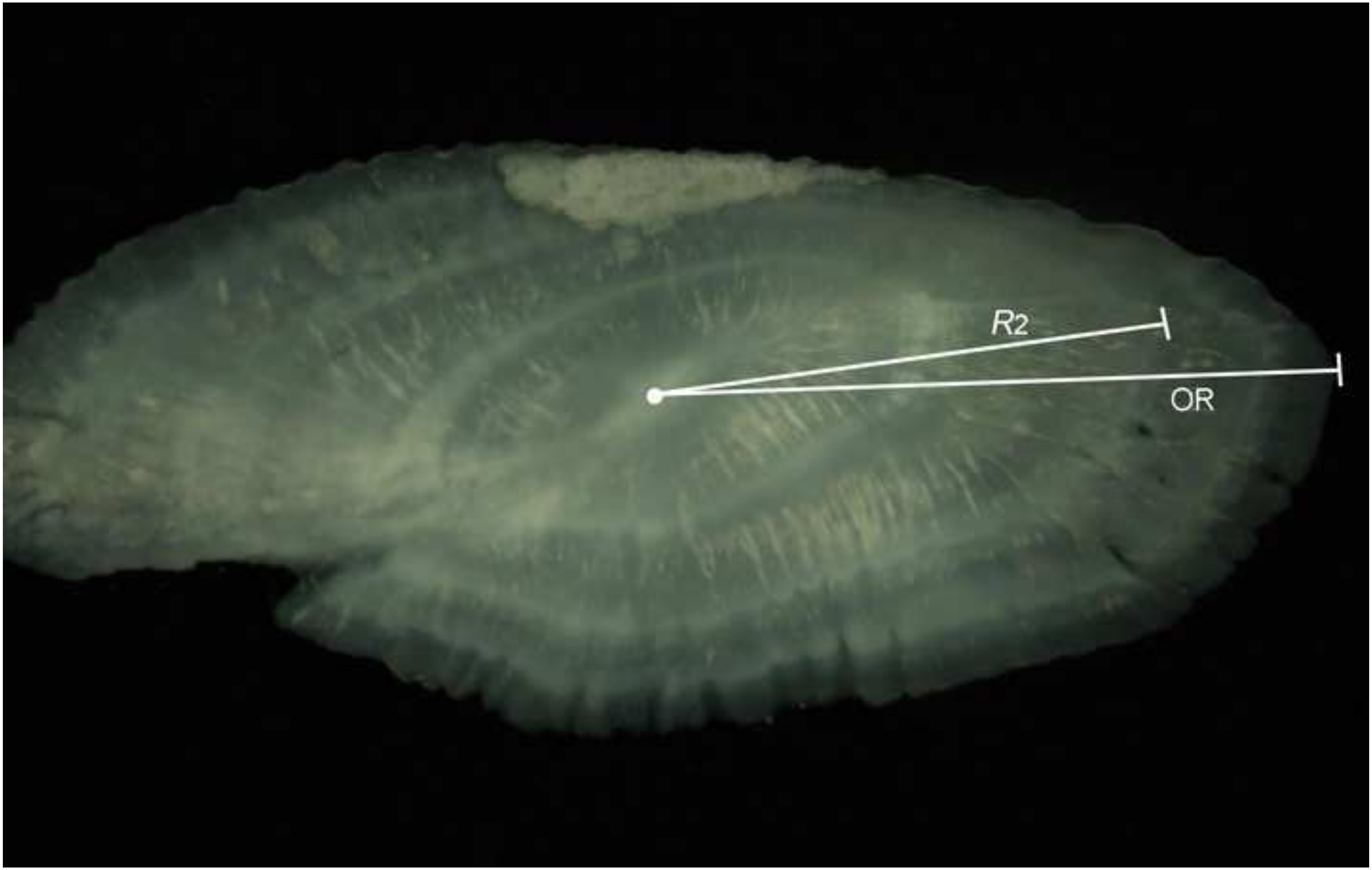
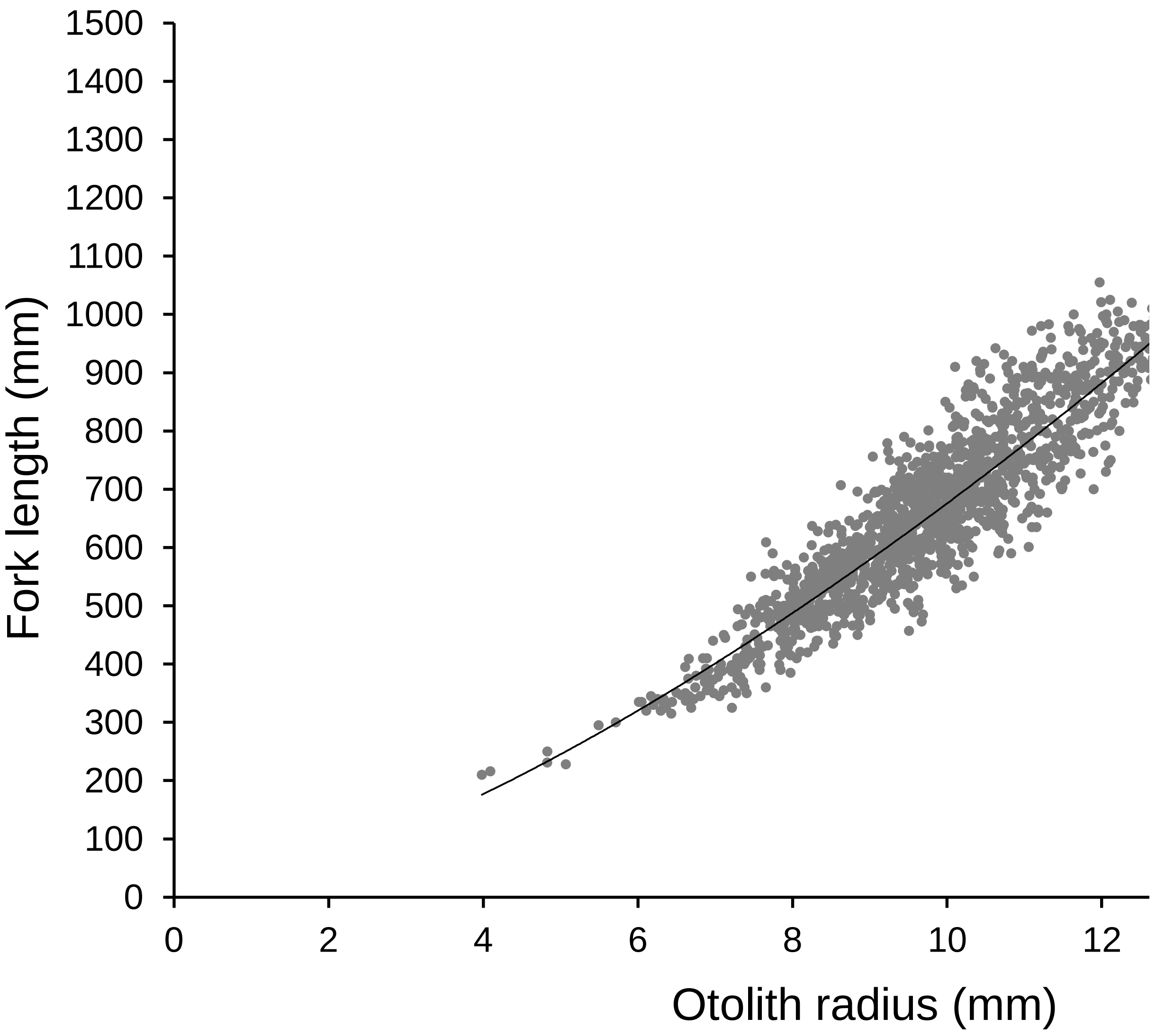
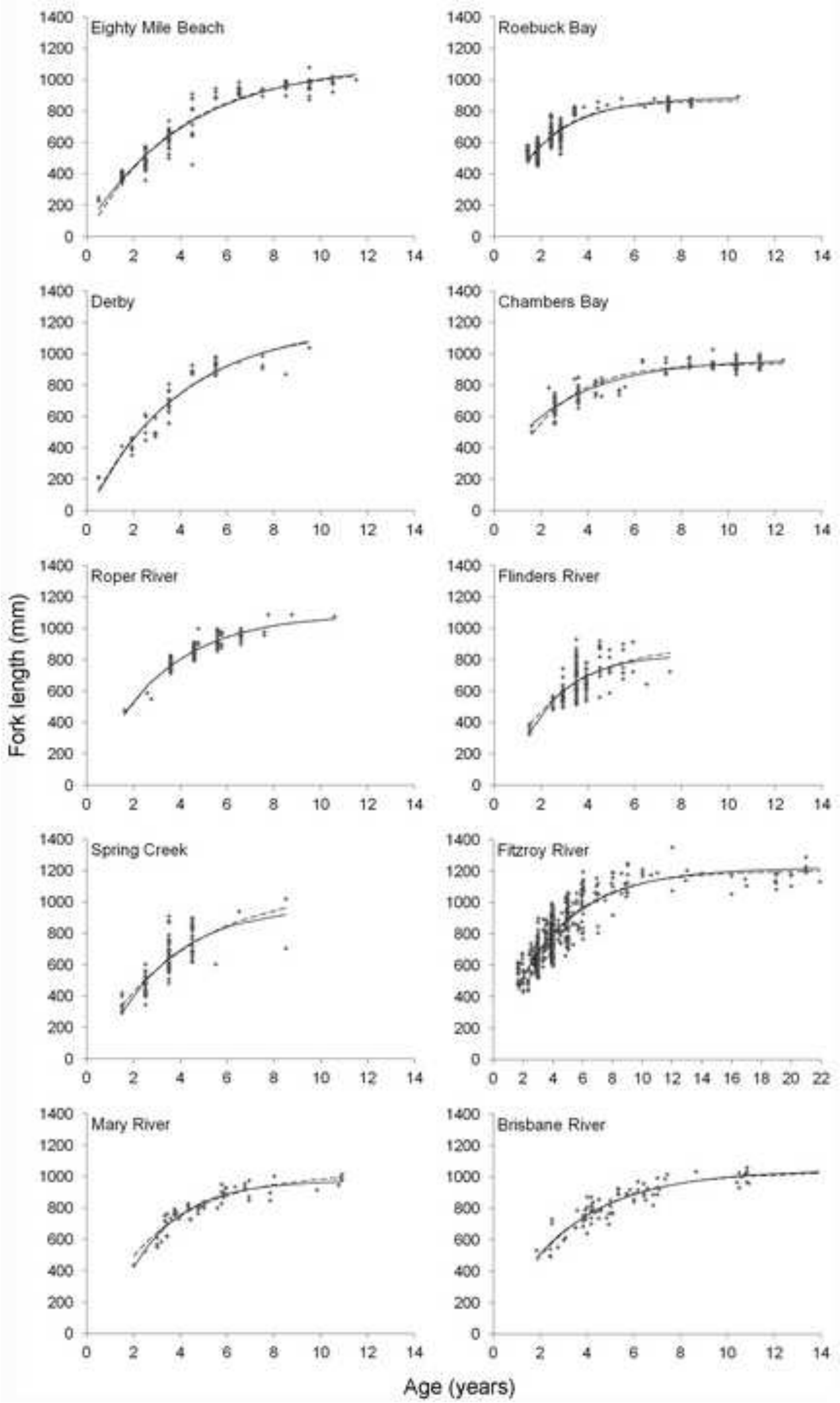


Figure 3



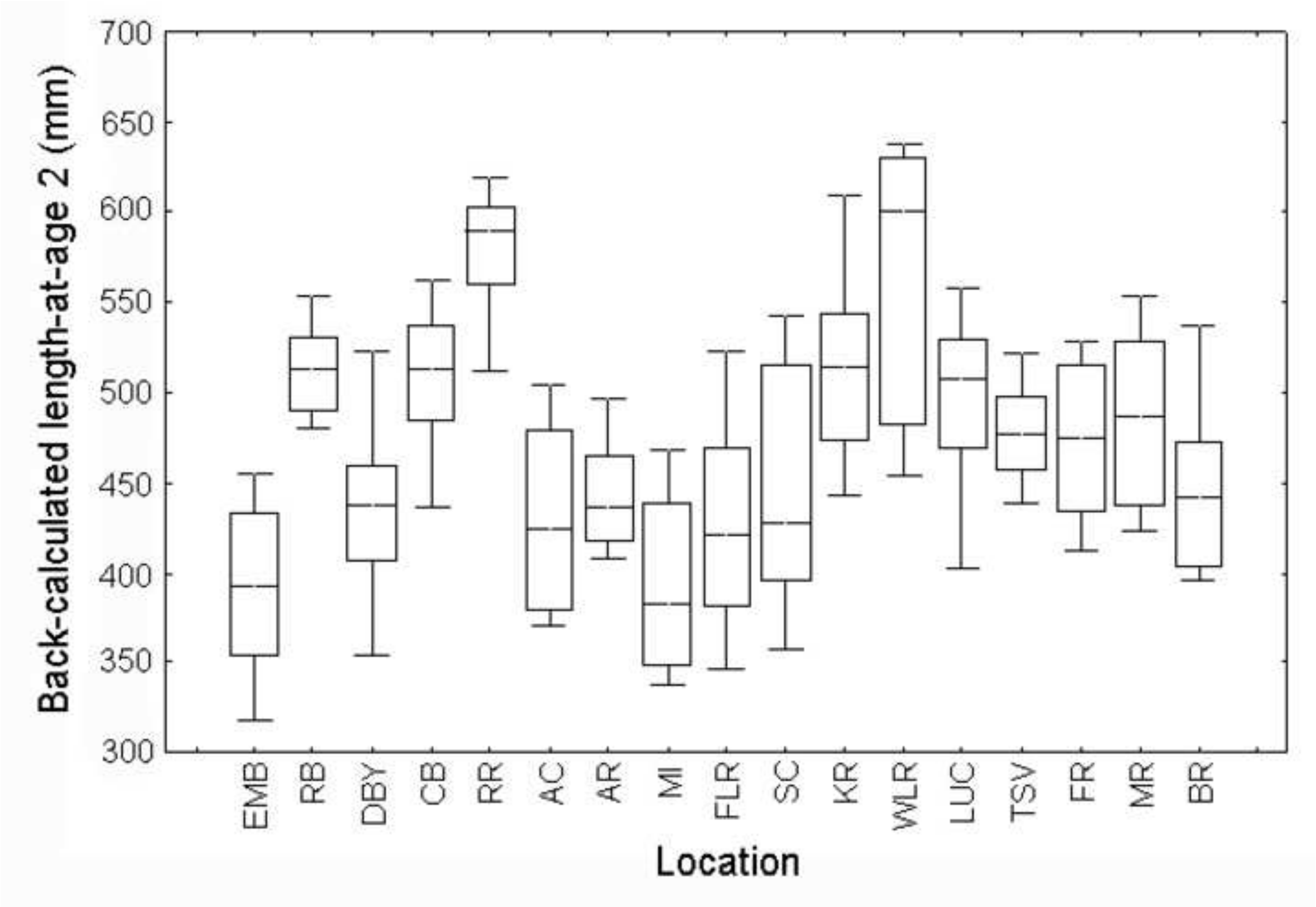
1500
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
Fork length (mm)
0
2
4
6
8
10
12
Otolith radius (mm)

Figure 4



Eighty Mile Beach
Roebuck Bay
Derby
Chambers Bay
Roper River
Flinders River
Spring Creek
Fitzroy River
Mary River
Brisbane River
Fork length (mm)
Age (years)
0
200
400
600
800
1000
1200
1400
0
2
4
6
8
10
12
14
16
18
20
22

Figure 5


Back-calculated length-at-age 2 (mm)
700
650
600
550
500
450
400
350
300
EMB
RB
DBY
CB
RR
AC
AR
MI
FLR
SC
KR
WLR
LUC
TSV
FR
MR
BR
Location

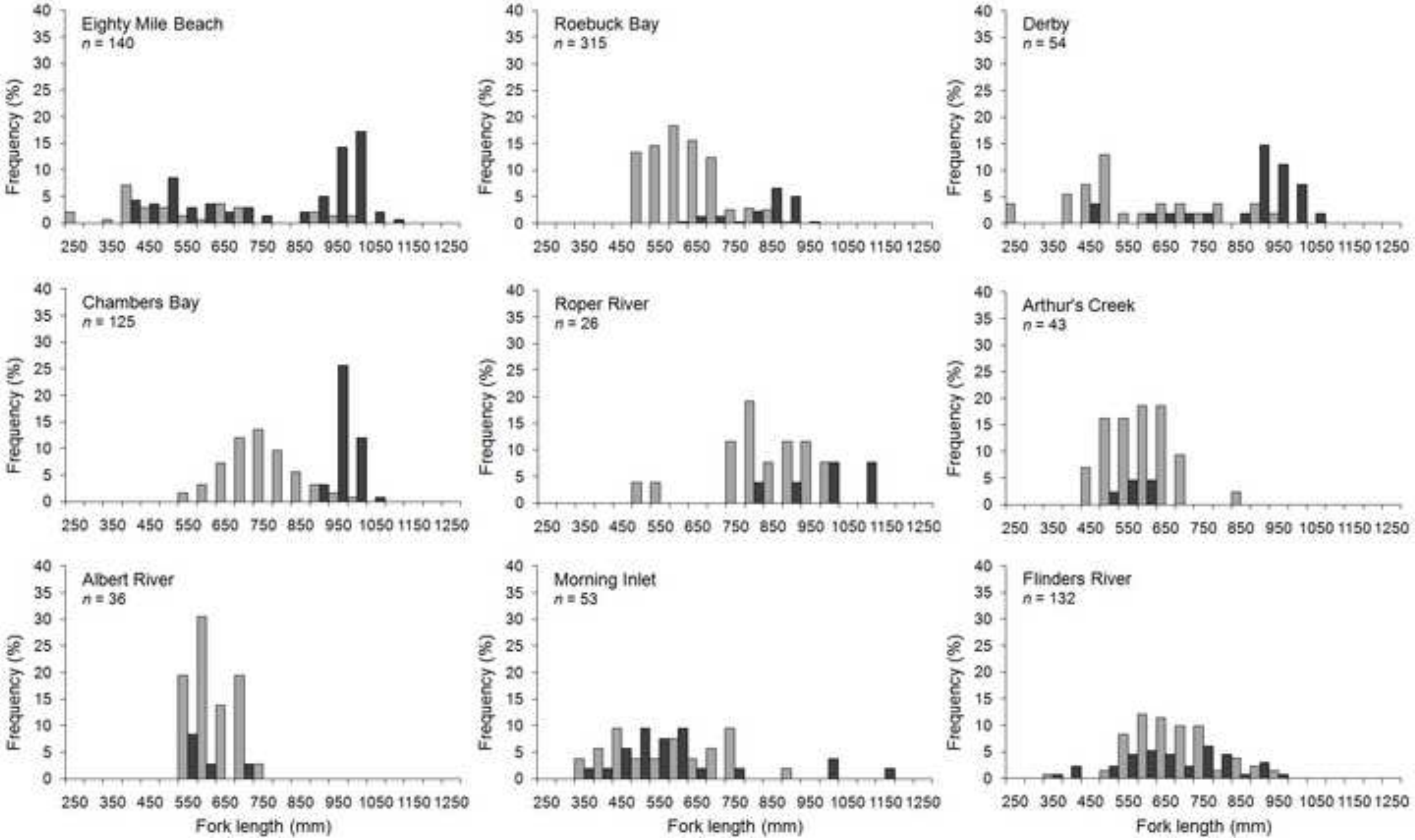

Eighty Mile Beach
n = 140
Roebuck Bay
n = 315
Derby
n = 54
Chambers Bay
n = 125
Roper River
n = 26
Arthur's Creek
n = 43
Albert River
n = 36
Morning Inlet
n = 53
Flinders River
n = 132
Frequency (%)
0
5
10
15
20
25
30
35
40
250
350
450
550
650
750
850
950
1050
1150
1250
Fork length (mm)

Figure 6 cont.

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