Do contemporary age-growth models overlook life-history complexities in protandrous fishes? A case study on the large protandrous polynemid, the giant African threadfin *Polydactylus quadrifilis*

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ABSTRACT

Sagittal otolith pairs were extracted from two-hundred-and-twenty-six giant African threadfin *Polydactylus quadrifilis* collected from the Kwanza Estuary in Angola between 2016 and 2018 ranging in size from 160 to 1360 mm fork-length (FL) and from one to 23 years of age (26 juvenile, 170 male, nine intersex and 27 female). An additional 85 otolith pairs (24 male, six female and 55 unsexed) were extracted in the same region between 2007 and 2014 (475−1525 mm FL, 2–23 years) and were utilised solely for modelling growth. Otolith aging revealed rapid growth and early maturation (L_{50} = 399.2 mm FL, A_{50} = 1.50 years). Sex change occurred over a wide size (790−1125 mm FL) and age (3–8 years) range and was initiated at 1082.3 mm FL and 6.2 years and completed at 1127.4 mm FL and 7.06 years. Strong evidence was provided for partial protandry in *P. quadrifilis* via the presence of several extremely old male fish, including one individual of 22 years and noticeable differences in length-at-age were observed between older male and female fish. To investigate potential life-history variability, three approaches were taken to group individuals and assess for improvements in model fit using the von Bertalanffy Growth Function (VBGF). Subgroups were determined by sex in Approach 1 and by predicted life-history pathway ('changers' & 'non-changers') in Approaches 2 (individuals on sex change pathways have increased growth following sex change) & 3 (individuals on sex change pathways have increased growth throughout ontogeny). In all approaches, differences were observed in the L_{∞} and k values between fish presumed to change sex and those presumed not to change sex. When compared to the conventional model produced for the entire population, all approaches produced considerably better model fit (Approach 1 = ΔAkaike Information Criterion (ΔAIC) = 64.7, Approach 2 – ΔAIC = 56.1 and Approach 3 – ΔAIC = 136.3) and Approach 3 produced better fit than Approach 1. This suggests that utilising conventional modelling techniques may be inappropriate for the stock assessment and management of sequential hermaphrodites and indicates that a revision of age-growth modelling techniques is required for species with multiple developmental pathways in order to maintain intrapopulation diversity and preserve resilience.

1. Introduction

In fisheries management, it is widely acknowledged that there is a need for a comprehensive understanding of the biology and life-history of the fisheries species at hand (Beverton and Holt, 1957; King and McFarlane, 2003). An important facet of this understanding relies upon the accurate aging of fish, as it allows researchers to investigate the growth patterns of individual species and populations and is valuable for

the assessment of population productivity, reproductive potential and sustainability over time (Higgins et al., 2015). Fish growth is often plastic, both within and amongst individuals, and can change in response to fishing pressure or other ecosystem or environmental change (Jennings, 1998; King and McFarlane, 2003; Moore et al., 2011). Monitoring for these biological changes can often provide an indication that populations may be under pressure (Heino and Godo, 2002) and therefore population-specific baseline estimates of important life-history characteristics need to be established as reference points to guide management decisions.

Traditionally, the life-history of species has been modelled under the assumption that the majority, if not all, members of the same species develop in the same way and maintain a similar life-history. However, it is evident that there is inherent variability in the evolutionary, ecological and behavioural characteristics within a species (Munday et al., 2006; Higgins et al., 2015; Crook et al., 2017; Reid et al., 2018). The most commonly addressed of those is the species-specific variability in life-history traits between male and female fish. This is often the result of marked differences in the behavioural and reproductive traits of males and females and thus their allocation of resources towards somatic growth is not the same (Gross, 1996).

Many fish species have complex life-histories and it is increasingly acknowledged that there are often numerous pathways for individual fish growth and sexual development both between and within sexes (Crook et al., 2017; Gross, 1996; Munday et al., 2006). This is further complicated in fish species with elaborate sexual patterns such as hermaphroditism. In hermaphroditic fishes, growth often varies according to the gender state of the individual and sex reversal is acknowledged as an energetically expensive process affecting somatic growth (Higgins et al., 2015). In sequential hermaphrodites, growth may differ between the primary and the terminal sex (Garratt et al., 1993; Munday et al., 2004) and the size and age at which sex change occurs is often highly variable (Munday et al., 2006; Pember, 2006). Sequentially hermaphroditic fishes may undergo sexual development through a variety of pathways. In some cases, not all individuals of the primary sex will transition into the terminal sex (Pajuelo et al., 2008), a phenomenon known as partial protandry in male-first hermaphrodites or partial protogyny in female-first hermaphrodites. Additionally, in other cases, not all members of the terminal sex will be derived from the primary sex (diandry in protogynous species and digyny in protandrous species) (Sadovy and Shapiro, 1987). These phenomena complicate the modelling of fish growth because it is only possible to assess the sexual state of an individual at the time of capture and it is most often impossible to accurately estimate the prior or future sexual function of said individual.

Despite this, growth models have been developed for many sequentially hermaphroditic fishes (Garratt et al., 1993; Munday et al., 2004; Pember, 2006), yet few publications have made any attempt at modelling and understanding the inherent life-history complexity present. Many of these models adopt the same technique that would be applied to a typical gonochorist species, producing a singular correlation between fish length and age based on all of the individuals within a population (e.g. Davis, 1984; Pember, 2006). In some cases, it may be argued that this is perhaps because the investigated species have not shown significant differences in growth which would have warranted further investigation. It may also be explained by the possibility that many of these species only (or at least largely) displayed one developmental pathway from the primary to the terminal sex at a specific age or size. Thus, a growth model describing the lengths-at-age for the whole population would adequately represent a high enough proportion of the population to ignore outliers created by a select few individuals with alternative life-history tactics or strategies (Higgins et al., 2015). Additionally, many researchers have provided separate relationships for fish of either sex, disregarding the fact that a proportion (or all) of the fish of the terminal sex are derived from the primary sex (e.g. Munday et al., 2004; Choat et al., 2006).

Regardless of the reasoning, the consequences of these techniques should be considered as we attempt to adequately describe the complex biological traits of fish species (Higgins et al., 2015). For example, certain sequential hermaphrodites may have numerous pathways for sexual development, each of which is affected differently by external selection pressures (Crook et al., 2017). If individuals on a specific developmental pathway exhibit slower growth rates than other fish on alternative pathways, for example, it is likely that management recommendations may not favour these fish. Since the maintenance of diversity, whether genetic, physiological, behavioural or life-history, is a central tenet of preserving the resilience of a species through the promotion of adaptive capacity (Elmqvist et al., 2003), the removal of fish belonging to a specific pathway will have consequences for the species. Therefore, describing the growth patterns of different developmental pathways and taking these into account in fisheries management is critical for the promotion of resilient fisheries.

The giant African threadfin *Polydactylus quadrifilis* (Cuvier, 1829) is a protandrous hermaphrodite (Butler et al., 2018) belonging to the teleost family Polynemidae. It is distributed along Africa's west coast from Angola northwards to Senegal and Mauritania (Motomura, 2004). Like many other polynemids (Longhurst, 1965; Moore et al., 2011; Motomura, 2004), *P. quadrifilis* occupies the brackish, and sometimes freshwater, reaches of rivers and estuaries at various stages during its life-history (Laë et al., 2004; Loubens, 1966, 1964; Moses, 2000; Simier et al., 2004). When in these environments, they are generalist predators, feeding largely on fish and crustaceans such as crabs, shrimp and prawns (Longhurst, 1957; Loubens, 1966) and have been reported to form near-shore spawning aggregations out at sea (Loubens, 1964).

Polydactylus quadrifilis plays an important role in recreational, subsistence and small-scale fisheries across its distribution (Butler et al., 2018; Loubens, 1964; Moses, 2000; Motomura, 2004). Despite the fisheries value of the species, its biology is largely understudied, excepting for a doctoral study undertaken in Gabon in the mid-1960s (Loubens, 1966). Furthermore, the protandrous nature of the species increases its susceptibility to overexploitation, via recruitment overfishing, as fishing practices often selectively remove the larger, in this case female, fish first from the population (Law, 2000) and generally reduce the number of fish that survive to an old age (Heino and Godo, 2002).

The protandrous nature of *P. quadrifilis* is likely to affect the growth between individuals over time as their somatic growth rate may vary according to their reproductive state at any given time (Higgins et al., 2015). To understand these differences, it is important to identify the various pathways that exist for individual sexual development. A recent reproductive investigation of the species (Butler et al., 2018), which identified the species as a protandrous hermaphrodite, noted that there were a small number of large males within the population whose size exceeded the size range in which sex changing fish were observed. Based on this observation, it was hypothesised that some proportion of primary male fish do not change sex and become female (partial protandry), however, it was recommended that a similar study with the additional utilisation of accurate age estimates would be needed in order to confirm this trait (Butler et al., 2018). Furthermore Butler et al. (2018) did not observe any small or juvenile female fish below the size range in which transitional individuals were found. Therefore, it seemed unlikely that primary females existed within the sampled group of fish, although they were unable to confirm with certainty whether the species is mono- or digynic.

This paper aims to investigate the life-history characteristics of *P. quadrifilis* in the Kwanza Estuary and explore the manner in which growth rates are represented in hermaphroditic fishes. Specific objectives included determining the size- and age-at-maturity and size- and age-at-sex-change for *P. quadrifilis*. Thereafter, alternative methods for adequately describing the growth of *P. quadrifilis* individuals belonging to either one of two distinct hypothetical life-history pathways: pathway I ('changers') – initial maturation as a primary male followed by a sex change to female; pathway II ('non-changers') – initial maturation as a

male fish with no subsequent sex change, was investigated using von Bertalanffy Growth Functions (VBGFs). It was hypothesized that models which include pathway-specific parameters explain more of the growth data than simple sex-specific or single population VBGFs.

2. Material and methods

Sampling took place in the mouth area and first four kilometres of the Kwanza Estuary in Angola between the 21st of June 2016 and the 31st of March 2018. Two hundred and twenty-six fish were either collected using conventional angling techniques or purchased from local subsistence gill-net and longline fishermen.

Once acquired, fish were weighed (nearest 0.01 kg) and measured (FL and TL, mm) before being dissected. Fish were sexed and the gonads were macroscopically staged according to the eight stages outlined by Laevastu (1965): I = virgin (males only); II = immature/resting; III = developing; IV = maturing; V = mature/pre-spawning; VI = spawning; VII = spent; VIII = recovering (Butler et al., 2018). The sagittal otoliths were removed and stored in paper envelopes for further processing and analysis.

Additionally, the sagittal otolith pairs from 83 *P. quadrifilis* (with measurement data; FL, mm) were collected from the same location between 2007 and 2014. These data were only included in assessing the overall growth of *P. quadrifilis* (VBGF).

2.1. Otolith preparation

To determine the optimal otolith sectioning protocol, a pilot study was conducted using a sub-sample of 60 otolith pairs. Otoliths from the same fish were either analysed whole in methyl salicylate, or after being transversely or longitudinally cut into 500 μm sections containing their primordia. Otoliths were set in clear polyester resin before being sectioned using a twin-blade diamond-edged geological saw and mounted on microscope slides using DPX mountant. For each analysis, the number of opaque zones between the otolith nucleus and edge were observed microscopically using reflected light and recorded by three independent readers. Additionally, each otolith reading was assigned a readability index value of between 0 (unreadable) and 5 (easily readable). The ideal sectioning method was selected based on the average of the readability indices (ARI) and the calculated index of average percentage error (IAPE - Beamish and Fournier, 1981):

$$IAPE = \frac{1}{n} \sum_{j=1}^{n} \left[\frac{1}{R} \sum_{i=1}^{R} \left| \frac{X_{ij} - \bar{X_j}}{\bar{X_j}} \right| \right]$$

where n fish are aged, R is the number of times each fish j is aged, X_{ij} is the ith age determined for the jth fish, and $\bar{X_j}$ is the average age calculated for the jth fish.

Based on the results of the pilot study, all subsequent otoliths were sectioned transversely at 500 μm. The entire otolith collection was read by two readers independently and thereafter reread by the first reader following a period of several weeks. On each occasion, the number of visible opaque bands were counted and the otolith edge type was classified according to Harris et al. (2007) and Burton et al. (2015): 1 – opaque zone on otolith edge; 2 – narrow translucent zone (<30 % of the width of the previous translucent zone); 3 – moderate translucent zone (30 %–60 % of the width of the previous translucent zone); 4 – wide translucent zone (>60 % of the width of the previous translucent zone). For all sections, the age of a fish was accepted when a) at least two of the three opaque zone counts were the same (e.g. 4, 4, 5 = 4) and b) for fish that were aged as 10 years or older, when the three counts were consecutive (e.g. 10, 11, 12), the middle reading (11) was accepted. Otolith edge type was accepted when at least two of the three classifications were the same (e.g. 1, 1, 2 = 1)

Age values were adjusted according to the edge type for each otolith.

Individuals that were captured during or soon after the period of opaque zone formation were assigned an age equivalent to the opaque zone count (edge types 1 – opaque zone on otolith edge; and 2 – narrow translucent zone). Otoliths with edge types 3 (moderate translucent zone) and 4 (wide translucent zone) were given an age equivalent to the opaque zone count plus one (Burton et al., 2015; Harris et al., 2007).

2.2. Age validation

The periodicity of opaque zone formation was validated using the mean edge type per month (Harris et al., 2007).

As further endorsement, a representative sample of 91 *P. quadrifilis* captured using conventional angling gear were injected intramuscularly with high-tet 120 oxytetracycline (OTC; 0.1 mL.kg^{-1}), tagged and released at the capture site. A single fish was recaptured after a period of 333 days at liberty. The otoliths from this individual were removed, transported and sectioned (as above) in the dark and observed and photographed at 40x magnification under ultraviolet (UV) light and under normal reflected light.

2.3. Models

2.3.1. Length- and age- at-maturity and at-sex-change

Macroscopic staging data were used to assess the length- and age-at-sexual maturity of sampled *P. quadrifilis*. Fish were considered mature when gonads were staged as III or above, based on the assumption that they would mature within the same spawning season. A modified logistic regression model (Walker, 2005) was used to estimate length- and age-at-maturity according to the following equations:

$$P(L) = P_{MAX}(1 + e^{-\ln(19)\left(\frac{L - L_{50}}{L_{95} - L_{50}}\right)})^{-1}$$

$$P(A) = P_{MAX}(1 + e^{-\ln(19)\left(\frac{A - A_{50}}{A_{95} - A_{50}}\right)})^{-1}$$

where P is the proportion of mature fish at a given fork-length (L) or age (A), L_{50} (or A_{50}) is the length (or age) at which 50 % of the fish have reached maturity, L_{95} (or A_{95}) is the length (or age) at which 95 % of the fish have reached maturity and P_{MAX} is the asymptote of the ogive. To estimate L_{50}, A_{50}, L_{95} and A_{95}, a generalised linear model (GLM) with a binomial error structure and a logit link function was fit to the relationship between maturity level (0 = immature,1 = mature) and age, using the '*lme4*' package (Bates et al., 2015) using Rstudio version 1.2.5033 (R Development Core Team). Ninety-five percent confidence intervals of the GLM parameters, L_{50}, A_{50}, L_{95} and A_{95}, were estimated using nonparametric bootstraps with 1000 replicates within the '*boot*' package (Canty and Ripley, 2016; Davison and Hinkley, 1997). When data were completely separated, GLMs were run within the '*BRGLM*' package (Kosmidis, 2017) using a bias reduction method (Firth, 1993) for accurate parameter estimates.

The lengths and ages at which 50 % and 95 % of individuals had either initiated or completed sex change was calculated using the same logistic regression model. In the first case, intersex fish were grouped with females due to the fact that they had either initiated (intersex) or completed (female) sex change. In the second case, intersex fish were grouped with males to assess the L_{50}, A_{50}, L_{95} and A_{95} at which sex change was completed. Because the aim of this analysis was to accurately estimate the L_{50}, A_{50}, L_{95} and A_{95} for fish that undergo sex change, males over the age of 10 years were excluded from the analysis under the assumption that they would not change sex.

2.3.2. Growth

The VBGF was chosen to model growth due its successful prior application for the majority of aged polynemid species (Dentzau and Chittenden, 1990; Longhurst, 1965; Pember, 2006; Prasad et al., 2005;

Sossoukpe et al., 2016). The VBGF was fitted to the full length-at-age data set (n = 311) using the following formula:

$$L(t) = L_\infty \left(1 - e^{-k(t-t_0)}\right)$$

where $L(t)$ is the fork-length of a fish at age t, L_∞ is the asymptotic maximum length for the population, k is the growth coefficient and t_0 is the x-intercept. The model was fitted using a non-linear regression function and parameters were estimated by minimising the sum of squares of the residuals using the '*nls*' function in Rstudio version 1.2.5033 (R Development Core Team). Model variability was calculated using parametric bootstrapping in which 1000 iterations for the parameter estimates were randomly computed using the '*nlsBoot*' function in the '*nlstools*' package (Baty et al., 2015). The 95 % confidence intervals for the parameters were calculated from the bootstrap data as the 2.5 and 97.5 percentiles of the corresponding estimated values (Buckland, 1984).

To consider separate subgroups within the population, group-specific parameters were allocated within the general VBGF as per the notation used by Ritz and Streibig (2008).

$$L(t) = \begin{cases} L_{\infty[1]}\left(1 - e^{-k[1](t-t_0[1])}\right) & \text{if in group 1} \\ L_{\infty[2]}\left(1 - e^{-k[2](t-t_0[2])}\right) & \text{if in group 2} \end{cases}$$

or

$$L(t) = L_{\infty[group]}\left(1 - e^{-k[group](t-t_0[group])}\right)$$

For subgroup analyses, only individuals with complete length, age and sex data were considered (n = 256). Three separate approaches were used to group fish according to sex or hypothetical life-history pathway.

Approach 1: Sex-specific model parameters

In order to group fish by sex, all juvenile fish (n = 26) were grouped with males (n = 194), based on the assumption that all juveniles would develop directly into males within a short period, and all intersex fish (n = 9) were grouped with females (n = 27), based on the assumption that all intersex fish would develop directly into females within a short period.

Approach 2 & 3: Life-history pathway-specific model parameters

The growth of individuals from the two hypothesised developmental pathways (pathway I, 'changers' – initial maturation as a primary male followed by a sex change to female and pathway II, 'non-changers' – initial maturation as a male fish with no subsequent sex change) was investigated. However, it was not possible to ascertain which pathway young juvenile and male fish would utilise, as it is possible that they may

still change sex to female at a later stage. Therefore, two different model approaches were taken, each with different assumptions for the hypothetical pathways. Based on the smaller sizes observed for male fish compared with female fish of the same age, it was assumed that changers grew at a faster rate than non-changers. However, it was not possible to estimate whether differences in growth occur after or prior to sex change. Therefore, fish growth was assumed to be equal for either pathway up until sex change in Approach 2 or different throughout development in Approach 3 (Fig. 1).

Approach 2: Individuals on sex change pathways have increased growth after sex change

The second approach investigated the possibility that sex change is associated with increased growth (Fig. 1). In doing so, it was assumed that primary male growth was equal for both pathways up to the calculated A_{50} at which sex change is initiated (Fig. 1). However, it was not possible to estimate which juvenile and male fish $<A_{50}$ should be allocated to either pathway. Therefore, juvenile and male fish with ages $<A_{50}$ were randomly allocated to either pathway I ('changers') or II ('non-changers'). All male fish with ages $>A_{50}$ were grouped into pathway II. All intersex and female fish were grouped into pathway I. As a result, pathway I contained 99 randomly allocated juvenile and male fish $<A_{50}$ at which sex change is initiated, nine intersex fish and 27 female fish (n = 135). The data set for pathway II contained 111 randomly allocated juvenile and male fish $<A_{50}$ at which sex change is initiated and ten male fish $>A_{50}$ at which sex change is initiated (n = 121). The model assumptions were as follows:

  (i) all intersex and female fish are derived from males,
 (ii) fish lifespan and mortality are equal for both pathways,
 (iii) growth in each pathway is of a monophasic VBGF form,
 (iv) The A_{50} for sex change is known with certainty,
  (v) fish growth up to the A_{50} for sex change is equal for both pathways (i.e. increased growth takes place after sex change), and
 (vi) male fish $>A_{50}$ for sex change will remain male.

Approach 3: Individuals on sex change pathways have increased growth throughout ontogeny

The third approach investigated the possibility that sex change is associated with differential individual growth throughout development (Fig. 1). The ratio of female to male fish above the A_{95} for sex change completion was calculated as 3:1. All fish in each age class, i.e. at each integer age, below the age corresponding with the A_{95} for sex change completion were divided according to size with the larger three-quarters of the data points grouped into pathway I ('changers') and the smallest quarter into pathway II ('non-changers'). All intersex and female fish were grouped into pathway I and only male fish were considered in
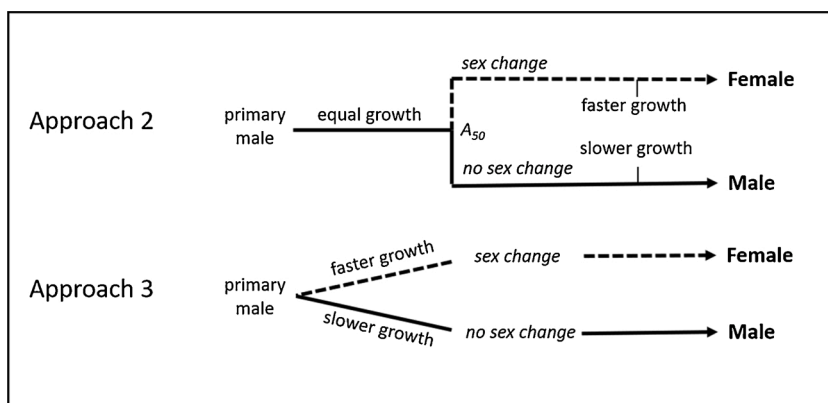

Fig. 1. Schematic diagram displaying the two approaches utilised to assess the potential drivers for sex change in *Polydactylus quadrifilis* and used to explain the various developmental pathways present. Approach 2 assumes that an increase in growth rate occurs following protandric sex change. The third approach assumes that growth varies naturally and that the fastest growing individuals change sex. Dotted lines represent pathway I ('changers') and solid lines represent pathway II ('non-changers'). Approach 1 involved grouping the sexes independently (all intersex and females in pathway I and all males and juveniles in pathway II) and is not displayed in the figure.

pathway II. All male fish above the age corresponding with the A_{95} for sex change completion were grouped into pathway II. As a result, pathway I contained 159 male fish $<A_{95}$ for sex change completion, nine intersex fish and 27 female fish (n = 195) The data set for pathway II contained 52 male fish $<A_{95}$ for sex change completion and nine male fish $>A_{95}$ for sex change completion (n = 61). Model assumptions were as follows:

Assumptions (i), (ii) and (iii) as outlined in Approach 2, and

(iv) The A_{95} for sex change is known with certainty,

(v) the ratio of fish belonging to each pathway is equal across all age classes and that the ratio is 3:1, changers:non-changers,

(vi) sex change pathways have different growth trajectories throughout ontogeny, and

(vii) male fish $>A_{95}$ for sex change will remain as males.

Within each approach, all possible reductions of the most complex VBGF were fit to the length-at-age data. The most complex model contained group-specific parameters for L_∞, k and t_0, while the simplest model contained only common parameters (i.e. the full VBGF applied to the whole population).

Model assumptions of normally distributed, homoscedastic residuals were tested on the most complex model in all cases as per Ogle (2013). All model variations were then compared using Akaike Information Criterion (AIC) with the 'best-fit model' having the lowest AIC value. Within each approach, models with ΔAIC < 2 of the lowest scoring model were considered as 'top scoring models' (Burnham and Anderson, 2004). The final model selection in each case was based on the 'top scoring model' with the fewest number of variables (Ogle, 2013).

3. Results

A total of 226 *P. quadrifilis* were sampled from 2016 to 2018 ranging in size from 160.0 mm to 1360.0 mm fork-length (FL), in mass from 0.05 kg to 40.7 kg and in age from one to 23 years (Fig. 2). Of these, the majority (n = 170, 75.2 %) were males (mean ± SD FL = 814.7 ± 138.2 mm; range: 436.0–1185.0 mm). The remaining fish sampled were comprised of females of larger size (n = 21; mean ± SD FL = 1193.1 ± 159.7 mm; range: 825.0–1360.0 mm), intersex fish (n = 9; mean ± SD FL = 954.1 ± 104.0 mm; range: 790.0–1125.0 mm) and juveniles (n = 26; mean ± SD FL = 244.2 ± 30.7 mm; range: 160.0–313.0 mm) (Fig. 2).

The additional 85 *P. quadrifilis* samples collected between 2007 and 2014 comprised fish ranging in size from 475 mm to 1525 mm FL and in age from two to 23 years. Of these, 24 fish were sexed as male, six as female and 55 were unsexed. These individuals were only included in the overall growth equation (VBGF).

Body-size relationships adhered to the following equations:

$TL = 1.1 \times FL + 27.2$ (n = 226, $r^2 = 0.99$)

$W = 5 \times 10^{-9} FL^{3.14}$ (n = 226, $r^2 = 0.99$)

3.1. Otolith preparation

Results of the pilot study indicated that transverse otolith sections provided a higher ARI value (4.0; longitudinal – 2.4; whole otoliths – 2.2) and a lower IAPE value (6.76) than longitudinal sections (25.05) or whole otoliths (40.13).

3.2. Age validation

Otolith sections displayed broad translucent zones and narrow opaque zones during the first 3–4 years of growth (Fig. 3a, b). Thereafter opaque zone formation occurred closer together resulting in narrower translucent zones (Fig. 3b). Agreement was good between readers and there was consensus between at least two of the three readings for the majority of otoliths (96.69 %). For the remaining 10 otoliths (3.31 %), where none of the three readings coincided, the three readings were consecutive (10, 11, 12) and the middle value was accepted. The IAPE score across the three readings for all otolith sections was 4.27 %.

The classification of otolith edge was accepted for all otoliths. Otolith edge analysis revealed that opaque zone formation occurred once annually (Fig. 4). *Polydactylus quadrifilis* in the Kwanza Estuary deposited opaque zones on the otolith marginal edge from July to February with a peak in November (Fig. 4). Narrow translucent zones (edge type 2) predominantly appeared in otoliths harvested from December to March. Moderate translucent zones (edge type 3) were identified in otoliths collected in the months from January until September (edge type 3) while wide translucent zones (edge type 4) predominantly appeared in otoliths collected from April until October prior to peak opaque zone formation in November (Fig. 4).

A single clear fluorescent band appeared in the sectioned otolith of the recaptured specimen (Fig. 3d). This fish was tagged on 4 August 2016 and recaptured on 3 July 2017 (333 days at liberty). During this time, the fish grew 125.0 mm from a FL of 905.0 mm at tagging to 1030.0 mm at recapture. The fluorescent band was positioned on the outer edge of a distinctive opaque zone (Fig. 3c, d). While there was no clear opaque zone present between the fluorescent band and the outer edge of the otolith, the distance between the fluorescent band and the otolith edge was equivalent to the distance between the two outer opaque zones (Fig. 3c, d).

3.3. Models

3.3.1. Length- and age- at-maturity and at-sex-change

Polydactylus quadrifilis displayed rapid maturation with all juvenile fish sampled (range: 160–313 mm FL) belonging to the 1-year age class. All fish belonging to subsequent age classes were mature (436–1360 mm FL). The length and age at which 50 % of the population were mature was calculated as 399.2 mm FL and 1.50 years. The length and age at which 95 % of the population were mature was calculated as 512.2 mm
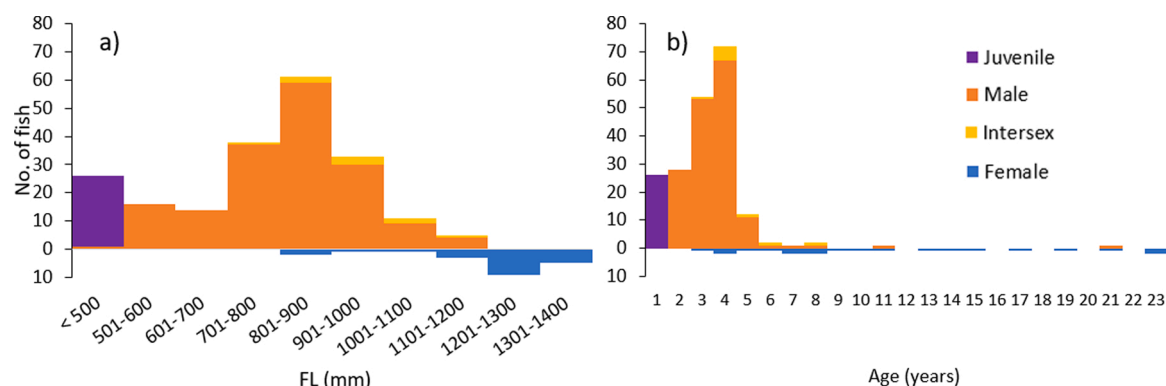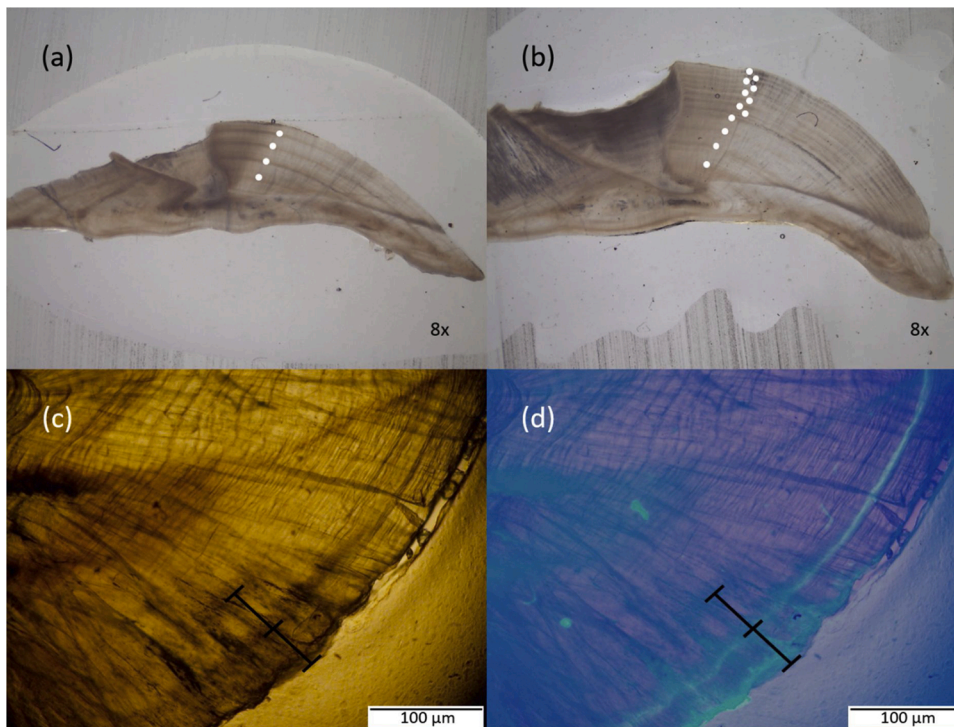

Fig. 2. Sex-specific length (a) and age (b) frequency histograms of 226 *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola.

Fig. 3. Photomicrographs of sectioned *Polydatylus quadrifilis* otoliths from a) a 5-year old (4 increments plus 1 – otolith edge type 4) 1010 mm FL male (August 2016), b) a 13-year old 1340 mm FL female (September 2017) and c) & d) a 6-year old recaptured intersex specimen following intramuscular injection of oxytetracycline (OTC; 0.1 mL.kg^{-1})(July 2017) under normal transmitted light (c) and ultraviolet light (d). The recaptured individual spent 333 days at liberty and grew from a FL of 905 mm at tagging to 1030 mm at recapture.
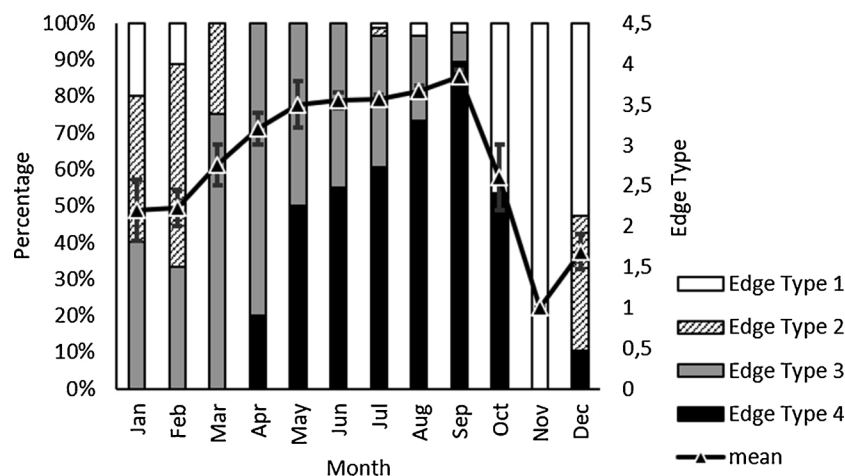

Fig. 4. Monthly percentage composition of otolith edge types and mean monthly edge score with standard error of *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. Edge types: 1 – opaque zone on otolith edge; 2 – narrow translucent zone (<30 % of the width of the previous translucent zone); 3 – moderate translucent zone (30 %–60 % of the width of the previous translucent zone); 4 – wide translucent zone (>60 % of the width of the previous translucent zone).

FL and 1.86 years, respectively.

The size and age at which sex change occurred within *P. quadrifilis* varied over a moderately wide range. Intersex individuals were observed at sizes ranging from 790 to 1125 mm FL and ages ranging from 3 to 8 years (Fig. 2). The length and age at which 50 % of the population had initiated or completed sex change was calculated to be 1082.3 mm FL and 1127.4 mm FL and 6.2 years and 7.06 years, respectively (Fig. 5a–d). The length and age at which 95 % of the population had initiated or completed sex change was calculated as 1309.4 mm and 1306.2 mm and 9.0 years and 9.8 years, respectively.

3.3.2. Growth

Growth in *P. quadrifilis* was adequately modelled by the VBGF (Fig. 6a; Table 1) and the estimated value of t_0 in the VBGF fitted to the full data set (0.23) confirms that the assigned ages are appropriate

(Table 1). The length-at-age noticeably differed between males and females of an old age (>7 years) (Fig. 6).

When separated by sex (Approach 1), the final accepted VBGF was the model with sex-specific parameters for L_∞ and k and common parameters for t_0 (Table 2, model 2.1) suggesting differences in growth and asymptotic size between males and females. Similarly, in Approach 2, the final model contained pathway-specific parameters for L_∞ and k and common parameters for t_0 (Table 2, model 3.1) suggesting differences in growth and asymptotic size between fish that change sex and those that do not, if increased growth takes place after sex change. In Approach 3, the most complex model, with pathway-specific parameters for L_∞, k and t_0 (Table 2, model 4), was accepted as the final model suggesting differences in growth, asymptotic size and size-at-birth between fish that change sex and those that do not, if sex change is associated with differential growth throughout ontogeny.
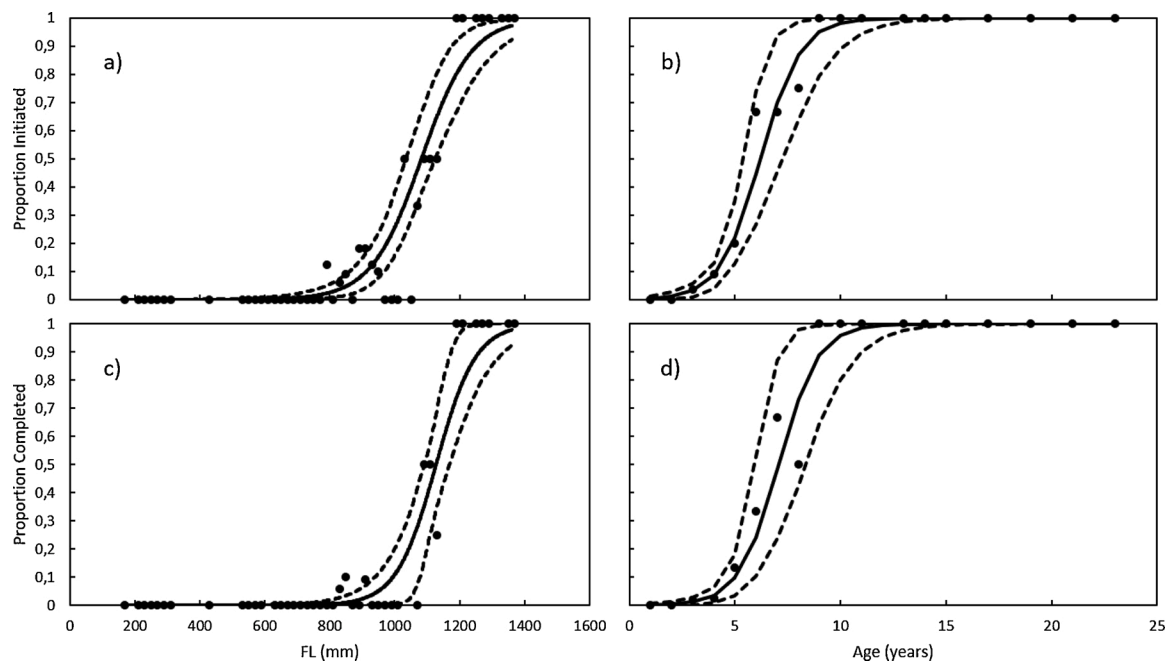
Fig. 5. Length- (a, c) and age- (b, d) at-sex change initiation (a, b) and completion (c, d) for *Polydactylus quadrifilis* collected from the Kwanza Estuary, Angola. Dotted lines represent the 95 % confidence intervals.
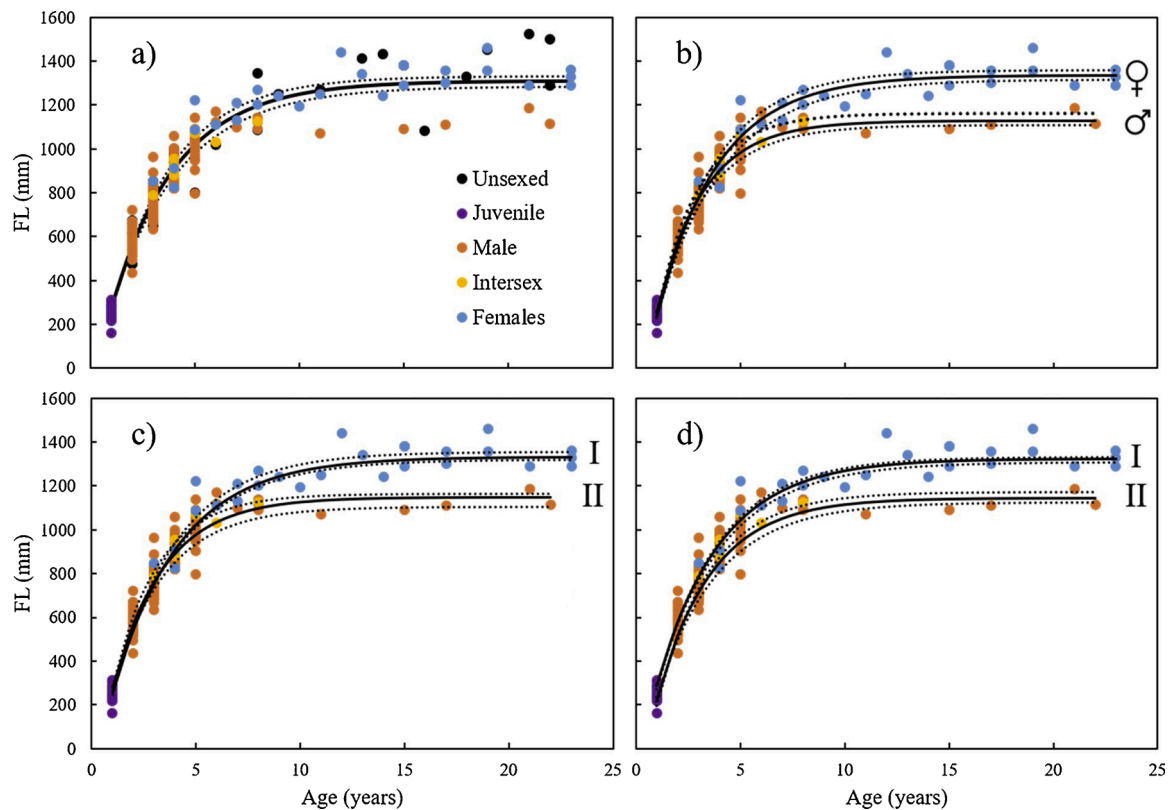

Fig. 6. Length-at-age (a) of 311 *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. A von Bertalanffy growth equation is fitted to all fish sampled ('full model') (a), to fish separated by sex in Approach 1 (juveniles and males vs intersex and females) (b) and to the two hypothetical developmental pathways, pathway I ('changers') and pathway II ('non-çhangers') for Approach 2 (c) and Approach 3 (d). For Approach 2 (c), male fish < A50 for sex change initiation (6.2 years) are randomly grouped into either pathways (I and II) and for Approach 3 (d), male data points < A95 for sex change (9.8 years) are grouped into either pathway according to size-at-age with the upper three-quarters grouped into pathway I and the lower quarter grouped into pathway II. All female and intersex fish are grouped into pathway I in both Approaches 2 and 3.

Table 1

Statistical values of the von Bertalanffy growth parameters for *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. Values are displayed for the full data set 'full model', for all female (and intersex) fish and all male (and juvenile) fish in Approach 1, and for the two developmental pathways, pathway I 'changers' and II 'non-changers', under the two hypothetical approaches (2 & 3) seen in Fig. 6.

		Summary Statistics				
		Parameter	Point estimate	Standard error	Median	2.5 % CI	97.5 % CI
	Full model (n = 311)	$L\infty$ (mm, FL)	1307.88	12.72	1308.48	1284.19	1332.53
		K (years^{-1})	0.32	0.01	0.31	0.30	0.33
		t_0 (years)	0.23	0.05	0.23	0.14	0.33
Approach 1	**All females (n = 36)**	$L\infty$ (mm, FL)	1335.76	14.27	1336.80	1314.78	1360.29
		K (years^{-1})	0.34	0.01	0.34	0.31	0.35
		t_0 (years)	0.43	0.04	0.43	0.37	0.48
	All males (n = 220)	$L\infty$ (mm, FL)	1131.52	18.09	1129.21	1106.29	1161.40
		K (years^{-1})	0.45	0.02	0.45	0.42	0.49
		t_0 (years)	0.43	0.04	0.43	0.37	0.48
Approach 2	**Pathway I 'changers' (n = 135)**	$L\infty$ (mm, FL)	1334.38	12.87	1331.06	1321.89	1354.75
		K (years^{-1})	0.31	0.01	0.31	0.31	0.33
		t_0 (years)	0.33	0.04	0.32	0.27	0.38
	Pathway II 'non-changers' (n = 121)	$L\infty$ (mm, FL)	1145.63	20.57	1147.07	1105.25	1166.29
		K (years^{-1})	0.42	0.02	0.41	0.40	0.46
		t_0 (years)	0.33	0.04	0.32	0.27	0.38
Approach 3	**Pathway I 'changers' (n = 195)**	$L\infty$ (mm, FL)	1320.83	7.13	1321.96	1309.87	1330.63
		K (years^{-1})	0.32	0.01	0.33	0.31	0.34
		t_0 (years)	0.25	0.05	0.25	0.19	0.33
	Pathway II 'non-changers' (n = 55)	$L\infty$ (mm, FL)	1146.60	15.22	1143.37	1126.58	1170.53
		K (years^{-1})	0.37	0.02	0.38	0.34	0.39
		t_0 (years)	0.44	0.07	0.46	0.32	0.54

Table 2

Various von Bertalanffy age-growth models for *Polydactylus quadrifilis* and their corresponding Akaike Information Criterion (AIC) values. Represented models include the full model based on all individuals (n = 256) (1), the sex-specific model in Approach 1 (2), the pathway specific model in Approach 2 (3) and the pathway specific model in Approach 3 (4). Reduced models are presented in cases where ΔAIC < 2.

		No.		d.f.	AIC
	'full model' ('fm')	1	$L(t) = L_{\infty(common)}(1 - e^{-k(common)(t - t0(common))})$	4	2852.984
Approach 1	'fm' with sex-specific parameters	2	$L(t) = L_{\infty(sex)}(1 - e^{-k(sex)(t - t0(sex))})$	7	2788.454
	'fm' with sex-specific $L\infty$ & k	2.1	$L(t) = L_{\infty(sex)}(1 - e^{-k}_{(sex)(t - t0(common))})$	6	2788.260
Approach 2	'fm' with pathway-specific parameters	3	$L(t) = L_{\infty(app1\_path)}(1 - e^{-k(app1\_path)(t - t0(app1\_path))})$	7	2796.443
	'fm' with pathway-specific $L\infty$ & k	3.1	$L(t) = L_{\infty(app1\_path)}(1 - e^{-k(app1\_path)(t - t0(common))})$	6	2796.919
Approach 3	'fm' with pathway-specific parameters	4	$L(t) = L_{\infty(app2\_path)}(1 - e^{-k(app2\_path)(t - t0(app2\_path))})$	7	2716.738*

Overall, Approach 1 (ΔAIC = 64.7), Approach 2 (ΔAIC = 56.1) and Approach 3 (ΔAIC = 136.3) achieved considerably lower AIC values than the full model (Table 2). Approach 3 produced the lowest AIC value overall, followed by Approach 1 and 2 (Table 2).

4. Discussion

The age-growth data presented, in combination with the sexual pattern information provided by Butler et al. (2018), gives strong evidence for partial protandry in *P. quadrifilis*. This was evident via the presence of several extremely old male fish, including one individual of 22 years, one year younger than the oldest female fish recorded. There also appeared to be an association between somatic growth and sex change whereby differences in the size of fish of the same age were observed between those that likely changed sex and those that did not, with older male fish noticeably smaller than females of the same age. This suggests that *P. quadrifilis* have at least two developmental pathways and it is likely that growth rate and asymptotic size of individuals varies between either pathway. In attempting to accurately model the two developmental pathways, further support was provided in that the best-fit models, providing the lowest AIC value, contained pathway specific $L\infty$ and k values in all approaches. Therefore, it is likely that fish that changed sex grew to larger sizes and at a faster rate than fish that did not change sex.

Somatic growth in *P. quadrifilis* was rapid in the first four years, with individuals reaching approximately 281.0, 558.6, 761.2, 909.1 and 1017.0 mm FL in their first, second, third, fourth and fifth years of growth respectively (based on the 'full model'). Individuals also displayed rapid sexual maturation as primary males after their first year of growth. Despite the grossly understudied nature of the biology of the majority of the Polynemidae, it would seem, from well-studied species, that fast growth and early maturation is common (Dentzau and Chittenden, 1990; Longhurst, 1965; Motomura, 2004; Pember, 2006). For example, Pember (2006) found that *P. macrochir* in Australia attained a size of approximately 827.8 mm TL in their fourth year of growth and reached maturity between 202 and 412 mm TL and at an age of between one and two years old.

In this study, sex change in *P. quadrifilis* was shown to occur within a broad size and age window ranging from 790 to 1125 mm FL and from 3 to 8 years. This broad window for sex change is common and has been observed in a number of sequential hermaphrodites (Munday et al., 2006) including members of the Polynemidae (*P. macrochir* range:

313–1139 mm TL and 2–8 years) (Pember, 2006). However, this suggests that sex change in *P. quadrifilis* is not closely related to age or size and is therefore more likely conditional to some other aspect of the individual state. If individual reproductive fitness is taken into consideration, then sex change would most likely be related to some property of the mating group and is probably associated with the ratio of primary males to secondary females and total egg to sperm biomass (Munday et al., 2006). However, sex change is also often related to social cues (Robertson, 1972; Shapiro, 1979) and without adequate information on other behavioural traits for *P. quadrifilis*, it is difficult to effectively understand what these may be.

From the two hypothetical models, it was clear that there is an association between sex change and somatic growth in *P. quadrifilis*. However, it was difficult to ascertain if this difference in growth between fish from the two developmental pathways took place prior to or after sex change, i.e. is increased initial growth a cue for sex change? Or do fish that change sex have increased growth rates as a result of their secondary female state? The evolutionary drivers involved in larger female size, in protandrous fishes, are most likely related to increased reproductive output (Ghiselin, 1969; Munday et al., 2006; Ross, 1990; Shapiro, 1987; Warner, 1988). Female *P. quadrifilis* exhibit significantly higher reproductive investment (higher GSI) when compared to males (Butler et al., 2018). As there is normally a trade-off between growth and reproductive output (Gross, 1996), it is surprising that secondary females, when compared with males, maintain faster growth and larger asymptotic size, despite having dedicated large energy reserves to the process of sex change as well as increased reproductive output. Hence, the most logical explanation for the increased growth rates of secondary female fish would be that increased growth took place prior to sex change, although this remains speculative. This scenario was hypothetically modelled in Approach 3, producing the best overall model fit (Table 2) and providing support for this theory.

While fast growth at a young age may be associated with sex change in this species, it is also possible that growth may accelerate after sex change, as demonstrated in Approach 2. In this case, the final model produced a higher AIC value than in Approach 3 (Table 2), suggesting less overall model fit. Additionally, Approach 2 produced a higher AIC value than Approach 1, the sex-specific model, and is therefore unlikely to accurately represent what is happening within the population. Therefore, it is unlikely that sex change results in increased somatic growth.

If sex change is related to accelerated growth in the primary male phase, then it would become critical to understand the factors affecting growth rate and whether they are determined by facultative or obligate drivers. In other words, is the variation in growth rate that may lead to a change of sex, or lack thereof, a result of the immediate surrounding environment (i.e. resource availability, favourable conditions, competitive ability etc.) and an individual's resultant state or is it caused by other factors stemming from a predestined genetic polymorphism? Essentially, this is an argument over the classification of strategy as 'conditional' in the first case versus 'alternative' in the second (see Gross, 1996).

Variable reproductive phenotypes related to differential growth are common in fishes and have been shown to result from both genetic polymorphism (e.g. *Xiphiphorous nigrensis*) and conditional strategy (e.g. *Salmo salar*), although the latter is far more common (Gross, 1996). A typical example would be that of male 'sneaking'. A number of fish species display two or more male phenotypes (Gross, 1996). Generally speaking, the first, and often more common, strategy involves high investment in growth over a longer period of time. This is directed at increasing desirable attributes related to display, courtship and fighting ability and often aimed at winning over females and reproductive rights. The second strategy invests highly in gonadal development with less investment in growth. These individuals are unable to compete directly with dominant males, but successfully reproduce by 'sneaking' mating opportunities.

Keeping this example in mind, it is possible that male *P. quadrifilis* which utilise developmental pathway II ('non-changers') invest more highly in reproductive output and less in somatic growth at a young age than those that utilise pathway I ('changers'). For example, it is possible that the majority of young *P. quadrifilis* primary males invest highly in somatic growth, with minor investment in reproduction; which is supported by the low relative GSI of small males compared with larger females (Butler et al., 2018). This is driven by the objective of growing rapidly, changing sex and then investing heavily in reproductive output at a larger size and as the sex with the reproductive advantage. However, this strategy is risky, as individuals will need to survive long enough to change sex and function as females in order to benefit. Therefore, a small proportion of primary male fish may invest relatively more energy into gonadal development as a tactic to combat sperm competition and increase individual reproductive success in the short-term. This 'choice' of strategy may be the result of two genetic phenotypes or it may be driven by conditional strategy (Gross, 1996) and may explain the observed patterns of growth in this study.

Alternatively, growth may simply vary naturally within the population, the result of both individual competitive ability (genetics) and resource availability, and individuals that grow rapidly change sex and become female while those that do not, remain male. In this case, two alternative tactics are displayed within a 'conditional strategy' (Gross, 1996). In the lower age cohorts, there is an obvious skew in sex ratio towards males. This may create an incentive for faster growing individuals to change sex and function as females due to the reproductive advantage it would provide them. However, at larger sizes, where the majority of primary males have completed sex change, the sex ratios are reversed and are skewed towards females. Within these cohorts, slower growers that have yet to change sex may not receive significant benefit by undergoing the energetically expensive process of sex change. These larger males also maintain higher reproductive output compared to small males due to their larger body size. Therefore, they may easily outcompete small males during spawning events, incentivising their male state. This theory also ties in well with the broad size and age range observed for sex change in *P. quadrifilis* and may therefore be the most likely scenario.

A similar theory was presented by Munday et al. (2004) for the protogynous parrotfishes *Scarus frenatus* and *Chlorurus sordidus*. Here, secondary males displayed faster growth and larger size than that of primary females. Otoliths for both sexes of both species were shown to increase in size consistently throughout life and not in direct accordance with somatic growth. The otoliths of secondary males were found to be smaller than those from females of the same size and this was put forward as evidence for a sex-specific growth effect, whereby the otoliths of faster growing individuals (changers) are smaller than in slower growers (non-changers). This effect was most pronounced during early life and it was therefore concluded that initial growth most likely dictated which fish changed sex, with faster growers changing, and slower growers remaining as females. Unfortunately, preliminary studies do not identify any similar size differentiation in the otoliths of *P. quadrifilis*.

The dearth of scientific research on *P. quadrifilis* inhibits the formation of robust conclusions about its life-history and there are undoubtedly numerous other aspects affecting an individual's growth. It would seem, from the little published information available, that the species has a strong dependency on the estuarine environment (Longhurst, 1957; Loubens, 1966, 1964) and migrates long distances up individual river systems (at least 250 km) (Laë et al., 2004; Simier et al., 2004). While sampling extensive Gabonese estuarine systems, Loubens (1966) reported extremely few juvenile fish below 20 cm standard length and therefore hypothesised that *P. quadrifilis* only migrate into the estuarine environment (from marine origin) at this size. Thereafter, he observed an increasing trend in the mean size range of fish as he sampled upstream, suggesting an upstream migration with initial development. However, larger, mature individuals were commonly located in close proximity to the ocean. From this, it would appear that *P. quadrifilis*

likely undertake largescale ontogenetic migrations and this is likely to have a large effect on somatic growth (Higgins et al., 2015).

Polydactylus quadrifilis utilise numerous highly variable habitats throughout their life-history and therefore it is possible that differences in the movement patterns between individuals may explain the observed variation in growth and an individual's resultant 'choice' of developmental pathway (Crook et al., 2017). Ontogenetic migrations are critical aspects that affect the life-history of fishes and have been found to have a significant relationship with the conditional strategy of an individual (Crook et al., 2017; Gross, 1996). The migratory behaviour of animals has received increasing amounts of attention in recent times and is acknowledged as being extremely complex (Reid et al., 2018; Secor, 2015). However, estuarine species provide unique opportunities for migratory study due to the fact that they are restricted to a narrow pathway upstream and downstream while within a system. In addition, movement into and out of the estuarine environment is easily monitored at a single location (Thorstad et al., 2013). This, in turn, greatly increases the ability of researchers to detect fish movement when using technology such as acoustic telemetry. Otolith microchemistry is also particularly useful for investigating ontogenetic movement between the marine and estuarine environment and it is recommended that the combination of these two fields, in a multi-method study of movement behaviour, would provide invaluable insights into the life-history of *P. quadrifilis* going forward.

The classification of life-history strategy is critical towards gaining an understanding of the evolutionary biology of a species but it is also, and perhaps more importantly, critical for fisheries conservation and management (Crook et al., 2017). Anthropogenic disturbances to the immediate environment including river abstraction, habitat alteration, climate change and harmful fishing practices have the potential to affect the composition of reproductive phenotypes within fish populations through their impact on the conditional strategies of individual fish (Crook et al., 2017). Through this, they can shift the points at which important life-history events, such as sex change, occur, thus affecting population growth rate, asymptotic size and overall reproductive capacity and population sustainability (Moore et al., 2011). Therefore, research focusing on the life-history of *P. quadrifilis* is critical for the appropriate management of the recreational, subsistence and small-scale fisheries of the region.

If the conventional techniques used to model fish growth are considered, the 'full model' and the separate models for 'all males' and 'all females' may not adequately represent life-history diversity for species with numerous developmental pathways. When compared to both Approaches 2 and 3 used in this study, it was shown that the 'full model' resulted in a considerably higher AIC value. Therefore, utilisation of a single model applied to the entire population may be highly inappropriate, in a similar manner to that of applying a single growth equation to a gonochoristic species with high sexual dimorphism.

The sex-specific model (Approach 1) provided a better alternative in this case and considerably reduced the AIC value compared with the full model, providing similar results to what was demonstrated in Approach 2 (Table 2). However, if two life-history pathways are indeed present within the population, then the sex-specific growth models cannot be entirely accurate as the male growth curve would represent fish from both pathways ('changers' and 'non-changers') simultaneously while the female growth curve would exclude early life-stage juvenile and male 'changers'. In this study, the lowest AIC value was observed in Approach 3 and, therefore, if differential growth in the primary male phase is associated with sex change, sex-specific growth models may not be adequate in order to comprehensively represent life-history diversity.

Going forward, it is important that fisheries scientists appreciate the complexities involved with modelling the growth of sequentially hermaphroditic species. Life-history variability needs to be further investigated and thereafter acknowledged and conserved through dynamic management plans. Adequate investigations of fish life-history need to be promoted so that they may be used simultaneously in age-and-growth

studies. Without the acknowledgement and appreciation of population diversity, we stand to drastically reduce the ability of fish populations to function and adapt to the ever-changing world we live in today. Through the appreciation and conservation of population diversity, it may be possible to preserve the resilience of fish species through the promotion of adaptive capacity, thereby building sustainable fisheries.

CRediT authorship contribution statement

Edward C. Butler: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing - original draft, Writing - review & editing. **Amber-Robyn Childs:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Resources, Software, Supervision, Validation, Writing - review & editing. **Marianne V. Milner:** Conceptualization, Funding acquisition, Visualization, Writing - review & editing. **Matthew W. Farthing:** Conceptualization, Data curation, Methodology, Writing - review & editing. **Murray I. Duncan:** Conceptualization, Formal analysis, Writing - review & editing. **Alexander C. Winkler:** Conceptualization, Methodology, Writing - review & editing. **Warren M. Potts:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

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