

REGULAR PAPER

The life-history of *Cheilodactylus rubrolabiatus* from south-western Australia and comparison of biological characteristics of the Cheilodactylidae and Latridae: support for an amalgamation of families

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Cheilodactylus rubrolabiatus collected from the south and lower west coasts of Western Australia were used to investigate the influence of habitat and environmental conditions on the biology of this species. A lack of difference in the growth *C. rubrolabiatus* from cool south coast and warmer lower west coast waters in Western Australia and the greater maximum ages attained by fish on the latter coast, both run contrary to premises of the metabolic theory of ecology (MTE). Although the greater size (L_{50}) and age (A_{50}) at maturity of *C. rubrolabiatus* on the south coast is consistent with MTE, this may reflect higher densities of fish on discontinuous shoreline rocky reefs on this coast and thus the need for fish, particularly males, to attain a larger size to successfully defend habitat and mates during spawning. Members of the closely related Cheilodactylidae and Latridae vary in maximum fork length (L_{Fmax} 280–950 mm) and age (19–97 years) and display a range of growth patterns. While the L_{50} of cheilodactylid and latrid species increased with increasing asymptotic lengths (L_{∞}), their maximum ages did not necessarily reflect the A_{50} (i.e., mature early, but live long). The M (natural mortality): k (von Bertalanffy growth parameter) ratios indicate that *Cheilodactylus* and *Nemadactylus* species exhibit a type II life-history strategy, typified by initial rapid growth, L_{50} close to their L_{∞} and little or no growth during an extended adult phase. A lack of distinct difference in the biological characteristics of the Cheilodactylidae and latrids may assist in resolving uncertainty regarding the taxonomy of these families.

KEYWORDS

growth, habitat, life-history strategy, longevity, maturation, spawning

1 | INTRODUCTION

The superfamily, Cirrhitidae, contains five families, the Cirrhitidae (hawkfishes), Chironemidae (kelpfishes), Aplodactylidae (marblefishes), Cheilodactylidae (morwongs) and Latridae (trumpeters) (Nelson *et al.*, 2016). Owing to their commercial and recreational importance, descriptions of the biology of species is restricted to those in the latter two families (Coulson *et al.*, 2010; Francis, 1981; Lowry, 2003). Currently, the Cheilodactylidae consists of 27 species belonging to four genera, the most speciose of those being the *Cheilodactylus* Lacépède 1803 (16 species) and *Nemadactylus* Richardson 1839 (seven species), while the Latridae (trumpeters), consists of

three genera (*Latridopsis* Gill 1862, *Latris* Richardson 1839 and *Mendosoma* Guichenot 1848) and five species. Cheilodactylids and latrids are distributed in temperate coastal marine waters in southern hemisphere regions of the Atlantic, Indian and Pacific Oceans, as well as in waters off China, Japan and the Hawaiian Islands (Allen *et al.*, 2006; Nelson *et al.*, 2016), but are particularly conspicuous members of rocky reef-fish communities in southern Australian waters (Burridge & Smolenski, 2004; Gomon *et al.*, 2008; Lowry & Cappel, 1999).

The redlip morwong *Cheilodactylus rubrolabiatus* (Allen & Heemstra 1976), attains a maximum total length (L_T) of 600 mm (Gomon *et al.*, 2008) and is a common species on inshore reefs from Coral Bay

($\sim 23^{\circ}$ S, 114° E) in north-western Australia to Ceduna ($\sim 32^{\circ}$ S, 134° E) in South Australia (Fairclough *et al.*, 2011; Harmen *et al.*, 2003; Hutchins, 2005; Hutchins and Swainston, 1986). While *C. rubrolabiatus* is regularly recorded in underwater censuses of fish communities in south-western Australia (Fairclough *et al.*, 2011; Hutchins, 2005; Watson *et al.*, 2005), it is often only recorded in small numbers, presumably due to its cryptic nature and its non-attractiveness to bait used for underwater baited video censuses. In the south-west corner of Western Australia, where there is a mixture of granite and limestone-based reefs, *C. rubrolabiatus* was only observed on high-relief limestone reefs (Harman *et al.*, 2003). While other cheilodactylids species are of moderate commercial and recreational importance (Haddon *et al.*, 2005; Lincoln Smith *et al.*, 1989; Norriss *et al.*, 2016), *C. rubrolabiatus* is rated poorly for its eating quality (Hutchins & Swainston, 1986; Swainston, 2010). Consequently, it is not targeted by fishers, although is occasionally taken by recreational spear fishers (P. Coulson, personal Observation, April, 2016).

Marine waters off the lower west coast of Western Australia are a transition area between warm, subtropical and cool temperate waters (Hutchins, 1994; Wernberg *et al.*, 2012; Williams *et al.*, 2001), largely due to the presence of the warm, poleward flowing Leeuwin Current (Pearce & Phillips, 1988; Pearce & Hutchins, 2009). While the south coast of Western Australia does experience the effects of the Leeuwin Current in years when this current is strong (Cresswell & Peterson, 1993), the south coast is typically temperate, being open to the influence of the Southern Ocean (Kendrick, 1999; Kendrick *et al.*, 2005a). In addition, reefs on the lower west coast comprise aeolianite limestone and form an interconnected series of islands and fringing reefs (Howard, 1989; Kendrick, 1999; Tuya *et al.*, 2009), while gneiss granite forms the basis of reefs, offshore islands and headlands that are interspersed by extensive open sand areas (Kendrick, 1999; Kendrick *et al.*, 2005a; Wells, 1990). Thus, despite their proximity, the lower west and south coasts of Western Australia exhibit differing environmental regimes that have been demonstrated to influence the biology of some teleosts whose distribution encompasses both regions (Cossington *et al.*, 2010; Coulson *et al.*, 2010; Lek *et al.*, 2012). Such environmental influence is also seen in the labrids *Semicossyphus pulcher* (Ayres 1854) and *Notolabrus fucicola* (Richardson 1840), the odacid *Odax pullus* (Forster 1801), the pomacentrid *Stegastes beebei* (Nichols 1924) (Cowen, 1990; Ruttenberg *et al.*, 2005; Trip *et al.*, 2014). In all cases, populations exhibit a cline in biological characteristics along a temperature and thus, also a latitudinal gradient, with individuals in cooler waters, although growing slower, attaining greater maximum lengths and ages and maturing at larger sizes and older ages. The effect of environmental temperature on the biology of ectotherms has been described as the temperature size rule (TSR), which reflects the influence of temperature on metabolic rate through the principles of the metabolic theory of ecology (MTE) (Atkinson, 1994; Angilletta *et al.*, 2004; Brown *et al.*, 2004; Charnov & Gillooly, 2004).

The current taxonomy of the Cheilodactylidae is contentious due to the uncertainty in the morphological divergence of the South African *Cheilodactylus fasciatus* Lacépède 1803 (Burridge & Smolenski, 2004). In addition, Greenwood (1995) suggested that

Nemadactylus species within the Cheilodactylidae be reassigned to the closely related Latridae, although morphological characteristics contradict this reassignment (Burridge & Smolenski, 2004; Smith, 1980). Furthermore, Burridge and Smolenski (2004) suggest that the Latridae should be expanded to include 17 members of the non-South African *Cheilodactylus* genus, which they showed not to be morphologically or genetically distinct from latrids. In addition, there was no defined trend in the relationship between life-history parameters (age at maturity vs maximum age; asymptotic length vs length at maturity) or growth patterns for a small number of *Nemadactylus* and *Cheilodactylus* species (Coulson *et al.*, 2010). The maximum fork lengths and ages of cheilodactylids and latrids range from 280–950 mm and 19–97 years (Ewing *et al.*, 2007; Mostacero *et al.*, 2003; Tracey and Lyle, 2005; Wöhler, 1996), while fork length and age-at-maturity estimates vary from 213–543 mm and 2.5–6.8 years (Stewart & Hughes, 2009; Tracey *et al.*, 2007; Wöhler, 1997b).

Biological characteristics of fishes, *i.e.*, maximum ages, length and age at maturity, are important when understanding the life history of a species. For example, longevity is an indication of the vulnerability of a species, with longer-lived species more vulnerable than shorter lived species due to their lower rates of natural mortality (Coulson *et al.*, 2009; Marriott *et al.*, 2007; Newman *et al.*, 2016). The relationship between life-history parameters have been used to provide parameter estimates for assessment modelling purposes (Beverton & Holt, 1959; Charnov, 1993) and to infer parameters from one another (Froese and Binohlan, 2000). These relationships, however, do not account for those species that mature at a relatively great length in comparison with their asymptotic size or those species which mature at an early age even though they attain a very old age (Coulson *et al.*, 2010, 2011; Prince *et al.*, 2014). A recent meta-analysis by Prince *et al.* (2014) demonstrated that a wide range of marine taxa, across trophic levels, display similar life-history strategies, *i.e.*, slow growth typically accompanies longevity. In this study, cheilodactylids were categorized as type II species, in which adults grow slowly and live to an old age, accumulating in larger size classes (Prince *et al.*, 2014).

The primary aim of this study was to provide a comprehensive description of the biology of *C. rubrolabiatus* from the south and lower west coasts of south-western Australia, regions that, although quite close, experience different environmental conditions. The collection of fish from the two coasts provided a basis for examining whether the biological characteristics of *C. rubrolabiatus* conformed to those of the TSR, *i.e.*, individuals of populations along on the cooler south coast grow slower, attain a greater maximum size and age and mature at a larger size and older age than on the warmer lower west coast. The life-history information determined in this study for *C. rubrolabiatus* was compared with the collated life-history information for other *Cheilodactylus*, *Nemadactylus* and latrid species, including species outside Australian waters that were not considered previously in the analysis by Coulson *et al.* (2010). This meta-analysis was used to investigate whether the biological characteristics of species in these families can be used to help elucidate taxonomic differences and thus provide further basis for their amalgamation (Burridge & Smolenski, 2004).

2 | MATERIALS AND METHODS

2.1 | Sampling regime and environmental measurements

Cheilodactylus rubrolabiatus were collected between March 2013 and September 2015 from coastal waters in Albany (~ 35° S, 118° E) and Bremer Bay (~ 34° S, 119° E) on the south coast of Western Australia and between June 2014 and December 2015 from coastal waters in Perth (~ 32° S, 116° E) on the lower west coast of that state. In waters off the south coast, fish were sampled over granite-based reefs along rocky shorelines, while in waters off the lower west coast fish were collected from along the limestone rock walls of harbours and around limestone-based islands and rocky reefs further offshore. In all cases, fish were sampled by spearfishing in depths <10 m.

2.2 | Length and mass measurements

A total of 421 and 358 *C. rubrolabiatus* were collected from the south and lower west coasts, respectively. The total length (L_T) and fork length (L_F) of each fish were recorded to the nearest 1 mm and their total mass (M_T) and gonad mass (M_G) recorded to the nearest 0.1 and 0.01 g, respectively. Lengths of individual fish were recorded as L_T to facilitated comparisons with other teleost species in the same region of south-western Australia, where lengths have traditionally been recorded as L_T (Coulson *et al.*, 2009, 2010, 2016; Cossington *et al.*, 2010; French *et al.*, 2014), while recording lengths as L_F enabled comparisons with other cheilodactylids where lengths have been recorded as L_F (Ewing *et al.* 2007; Jordan 2001; Lowry, 2003; Murphy & Lyle 1999; Stewart & Hughes 2009). Analysis of covariance (ANCOVA), employing M_T as the dependent variable and L_T or L_F as the independent variables and sex or coast as the fixed factor, was employed to determine if the relationships between M_T and both L_T and L_F were significantly different between sexes on each coast and between corresponding sexes on different coasts. A Kolmogorov-Smirnov (K-S) test was employed to determine whether the length compositions of the corresponding sexes of *C. rubrolabiatus* collected from the south and lower west coasts were significantly different.

2.3 | Age determination and growth

The otoliths of all *C. rubrolabiatus* collected, except those 34 individuals whose otoliths were damaged during capture by spear fishing, were sectioned, prior to reading, in order to clearly reveal all opaque zones, as was the case in previous ageing studies of cheilodactylids (Coulson *et al.*, 2010; Ewing *et al.*, 2007; Jordan, 2001; Lowry, 2003; Stewart & Hughes, 2009). The methods for the preparation, sectioning and reading of otoliths follows that described in Coulson *et al.* (2010) for another cheilodactylid, *Nemadactylus valenciennesi* (Whitley 1937). All counts and measurements were made on the ventral side of the otolith (Figure 1). Analyses of the trends exhibited throughout the year by the marginal increments on otoliths (i.e., the distance between the outer edge of the single or outermost opaque zone and the otolith periphery) were used to validate that a single opaque zone is formed annually in the otoliths of *C. rubrolabiatus*. The marginal increment

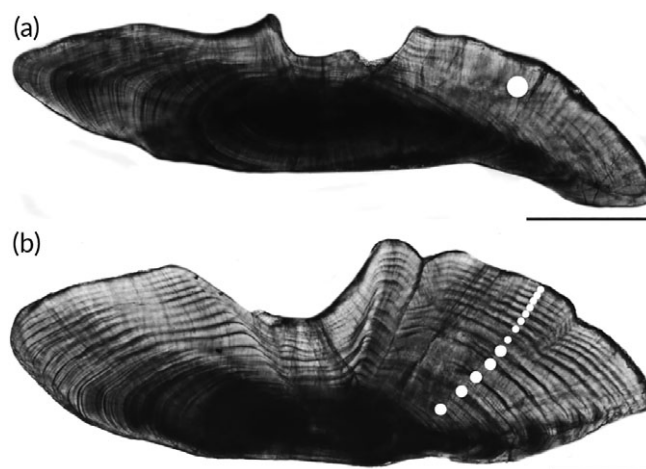


FIGURE 1 The sectioned otoliths of two individual *Cheilodactylus rubrolabiatus* with a 1 and b 13 opaque zones (O). Scale bars 0.5 mm

was expressed as a proportion of either the distance between the primordium and the outer edge of the single opaque zone, when one such zone was present, or of the distance between the outer edges of the two outermost opaque zones when two or more such zones were present. All distances were measured to the nearest 0.01 mm and along the same perpendicular axis to the opaque zones.

The approach described by Okamura and Semba (2009), but modified by Coulson *et al.* (2016), was applied to determine the periodicity of occurrence of otoliths with marginal increments falling within the lower 30 percentile of values for each category of zone counts. For this, binomial models, linked with von Mises circular distributions, were fitted assuming (a) no cycle, (b) an annual cycle or (c) a biannual cycle. The models were then compared using the Akaike information criterion (AIC), where the model with the smallest value was selected as best representing the data (Burnham & Anderson, 2002).

In order to assess the accuracy in obtaining counts of opaque zones from the otoliths of *C. rubrolabiatus*, the number of opaque zones in each sectioned otolith made counted by the author were compared with those obtained independently by another experienced reader of otoliths (E. C. Ashworth, Murdoch University) for a subsample of 100 *C. rubrolabiatus* otoliths, covering a wide size range. The level of precision was assessed using the coefficient of variation:

$CV_j = 100 \left(\sqrt{\sum_{i=1}^R (X_{ij} - X_j)^2 (R-1)^{-1}} X_j^{-1} \right)$, where CV_j is the age precision estimate for the j th fish, X_{ij} is the i th age determination of the j th fish, X_j is the mean age estimate of the j th fish and R is the number of times each fish is aged (Campana, 2001; Chang, 1982).

Each fish was assigned an age, based on the number of opaque zones in the otolith examined, but taking into account the time when the single or outermost of those zones become delineated, the date of capture of the fish and the average birth date (approximate mid-point of the spawning period) of 1 July assigned to the members of the populations on both coasts (see §3). von Bertalanffy growth curves (vBGC) were then fitted to the total lengths at age of the females and males of *C. rubrolabiatus* using the Newton-Raphson method and employing the non-linear regression routine in SPSS (2001). In the von Bertalanffy growth equation (VBGE): $L_T = L_{\infty}(1 - e^{-k(t-t_0)})$, where L_T is the total length (mm) at age t (years), L_{∞} is the asymptotic

total length (mm) predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length. vBGCs were also fitted to L_F at age of all female and all male *C. rubrolabiatu*s using the same method as mentioned above to facilitate comparisons with other Cheilodactylids.

A likelihood-ratio test was used to compare the vBGCs of the females and males on both coasts. The test statistic was determined as twice the difference between the log-likelihoods obtained by fitting separate growth curves to the L_T at age for each sex and by fitting a common growth curve to the L_T at age for females and males collectively (Cerrato, 1990). The hypothesis that the growth of the two groups could appropriately be represented by a single growth curve was rejected at the $\alpha = 0.05$ level of significance if the above test statistic exceeded $\chi^2_{\alpha}(q)$, where q is the difference between the numbers of parameters in the two approaches, i.e., 3 (Cerrato, 1990). The log-likelihood, λ , for each curve, ignoring constants, was calculated as: $\lambda = -n^{-2} \ln (sn^{-1})$, where n is sample size, s refers to the residuals of the sum of squares between the observed and expected lengths at age.

2.4 | Duration and prevalence of spawning

The sex of all fish was identified macroscopically, except for three fish from the south coast (L_T range 132–147 mm) and three fish from the lower west coast (L_T range 79–88 mm). Based on their macroscopic characteristics, the ovaries or testes of all other fish were assigned to one of the following four maturity stages adapted from the criteria used by Laevastu (1965): I–II, immature–resting; III–IV, developing–maturing; V–VI, prespawning–spawning; VII–VIII, spent–recovering. Individuals with stages III–VIII gonads in each year were considered likely to become mature (stages III–V) or to have matured (VI–VIII) because of the relatively discrete spawning time (see §3 and §4) and have thus been classified as mature for the purpose of determining size and age at maturity (see below). In each month of sampling, gonads from a subsample ($n = 5$ –10) of each sex and which encompassed all gonad stages recorded in that month, were used to confirm histologically that gonads had been macroscopically assigned to the appropriate stage of maturity. Gonads were thus placed in Bouin's fixative for either 24 or 48 h (depending on their size), dehydrated in a series of increasing concentrations of ethanol, their mid-regions embedded in paraffin wax, cut into 6 μm transverse sections and stained with Mallory's trichrome (Coulson et al., 2009; French et al., 2014).

Mean monthly gonado-somatic indices (I_{GS}) were determined for female and male *C. rubrolabiatu*s on both the south and lower west coasts with lengths \geq their corresponding L_{T50} at maturity (see below), using the equation: $I_{GS} = MG/MT \times 100$, where M_G is wet gonad mass and M_T is (total) wet body mass. The prevalence of the females and males with gonads at each developmental stage in each month was used in conjunction with monthly trends exhibited by the I_{GS} , to define the spawning period of *C. rubrolabiatu*s and helped elucidate its peak.

The L_T at which 50% and 95% of both the females and males of *C. rubrolabiatu*s (L_{T50} and L_{T95} , respectively), together with their 95% confidence limits, were determined by logistic regression analysis, as in previous

studies (Coulson et al., 2005, 2017). Logistic regression analyses for each sex in each region were restricted to data obtained during the main part of the spawning period (i.e., May–August). The form of the logistic model relating the probability, P , that a female or male *C. rubrolabiatu*s is mature to its L_T was: $P = 1 + e^{(-\ln 19(L_T - L_{T50})(L_{T95} - L_{T50})^{-1})}^{-1}$, where p is the proportion mature, L_T is the total length (mm) and L_{T50} and L_{T95} are the total lengths (mm) at which 50% and 95% of fish were mature, respectively. The L_F at which 50% and 95% of both the females and males of *C. rubrolabiatu*s (L_{F50} and L_{F95} , respectively), together with their 95% confidence limits, were also determined by the same logistic regression analysis to enable comparisons with other cheilodactylids.

A likelihood-ratio test was used to determine whether the L_{T50} for female *C. rubrolabiatu*s exceeded that of males on each coast, assuming a common value of for each sex and whether the L_{T50} for females or males on the south coast exceeded that of the corresponding sex on the lower west coast, assuming a common value of for each coast (Coulson et al., 2005, 2017).

2.5 | Life history characteristics of the Cheilodactylidae and Latridae

The life history characteristics of 11 members of the Cheilodactylidae and Latridae were obtained from the published literature. While the biological information for *C. variegatus* and *Latridopsis ciliaris* (Forster 1801) were available, the age and growth data for these species were not included in any analyses, for the following reasons. In the case of *C. variegatus*, ages were determined from counts of opaque zones in whole otoliths (Mostacero et al., 2012), which have been shown in other cheilodactylid species to lead to underestimates of age (Coulson et al., 2010; Ewing et al., 2007; Jordan, 2001; Lowry, 2003; Stewart & Hughes 2009). Samples of *L. ciliaris*, used by Jiang (2002), were collected from shallow, inshore waters and thus, do not include the full size and age range of this species, while Francis' (1981) study of *L. ciliaris* did not include growth parameters and his maturity estimates could not be confirmed due to lack of fish in the transitional size range. In addition, Francis (1981) acknowledges that the oldest fish of 20 years found in his study is not the oldest individual of this species.

Froese and Binohlan (2000) developed equations for the relationships between size at maturity (L_{F50}) and asymptotic size ($L_{F\infty}$) and between maximum age (A_{\max}) and age at maturity (A_{50}), based on the data for 265 fish species. The values for these biological parameters for members of the Cheilodactylidae and Latridae, where available, were inserted into these equations to investigate whether the relationship between these parameters for these species lay within the bounds of what would be expected based on those data for 265 fish species. In addition, estimates of the instantaneous rates of the natural mortality (M) of females and males of each species, except *C. variegatus* and *L. ciliaris*, were calculated by inserting the maximum recorded age of each sex into the equation of Hoenig (1983), which was then used when obtaining the M - k ratio, k being the VBGE parameter (Beverton & Holt, 1959). A high $M:k$ typifies those species that have a high natural mortality rate, fast growth and early maturation (i.e., engraulids and clupeids), while the reverse is true for species with a low $M:k$ (i.e., orange roughy *Hoplostethus atlanticus* Collett

1889). The value of this ratio was used to apply a life history classification to each species (Prince *et al.*, 2014)

3 | RESULTS

3.1 | Interpretation of otoliths and age validation

Two small *C. rubrolabiatus* measuring 79 and 88 mm L_T were caught in September (early austral spring) and another measuring 82 mm L_T was caught in November (late spring). The otoliths of these three individuals largely consisted of an opaque nucleus surrounded by a thin translucent margin. The translucent margins of the otoliths of the numerous small individuals caught between December (mid-summer) and 8 months later in August (late winter), increased in width. The otoliths of *C. rubrolabiatus* measuring 180–230 mm L_T and 168–288 mm L_T ($n = 17$), caught in the following September and October (early to mid-spring), respectively, also possessed an opaque nucleus surrounded by a wide translucent zone, but with an opaque zone now forming on the otolith edge. This opaque zone became delineated from the edge of the otolith, with a thin second translucent zone present on the edge of the otoliths of individuals measuring 256–316 mm L_T and 231–368 mm L_T caught in the following November and December ($n = 11$). As the proposed birth date for *C. rubrolabiatus* is July 1, *i.e.*, mid-winter (see later), the very small individuals caught in the initial September and November were *c.* 3 and 5 months old, respectively, while those caught in November and December, the following year, with a delineated opaque zone in their otoliths, were *c.* 17 and 18 months old, respectively. Therefore, the first opaque zone is laid down in the otoliths of *C. rubrolabiatus* during the second spring of life when fish are *c.* 15–16 months old.

A CV of 3.6% for the comparison of the counts of opaque zones in the otoliths of *C. rubrolabiatus* between two readers demonstrates the strong reproducibility of the counts between readers. The mean monthly marginal increments for otoliths of *C. rubrolabiatus* with 1 opaque zone increased from 0.15 in January to a maximum of 0.31 in October, before declining rapidly to 0.11 in December (Figure 2). While the mean monthly marginal increments for otoliths with 2–5 and ≥ 6 opaque zones followed a similar trend to that for fish with one opaque zone and thus increased from low levels in February, their maximums were attained slightly early in September and November, respectively (Figure 2).

The validity that the mean monthly marginal increments for *C. rubrolabiatus* followed a single cycle during the year is substantiated by the results of circular distribution models (Coulson *et al.* 2016; Okamura & Semba 2009). The AIC values for the models for the three groups of otoliths for fish on both coasts were less for an annual cycle than for no cycle or a biannual cycle (Table 1). In addition, the difference between the lowest AIC and each of the other two AICs for each group of otoliths exceeded 2, the number required to identify definitively the best model in terms of the Kullback–Leibler distance (Burnham & Anderson, 2002). The number of opaque zones in sectioned otoliths can thus be used for ageing individuals of *C. rubrolabiatus*.

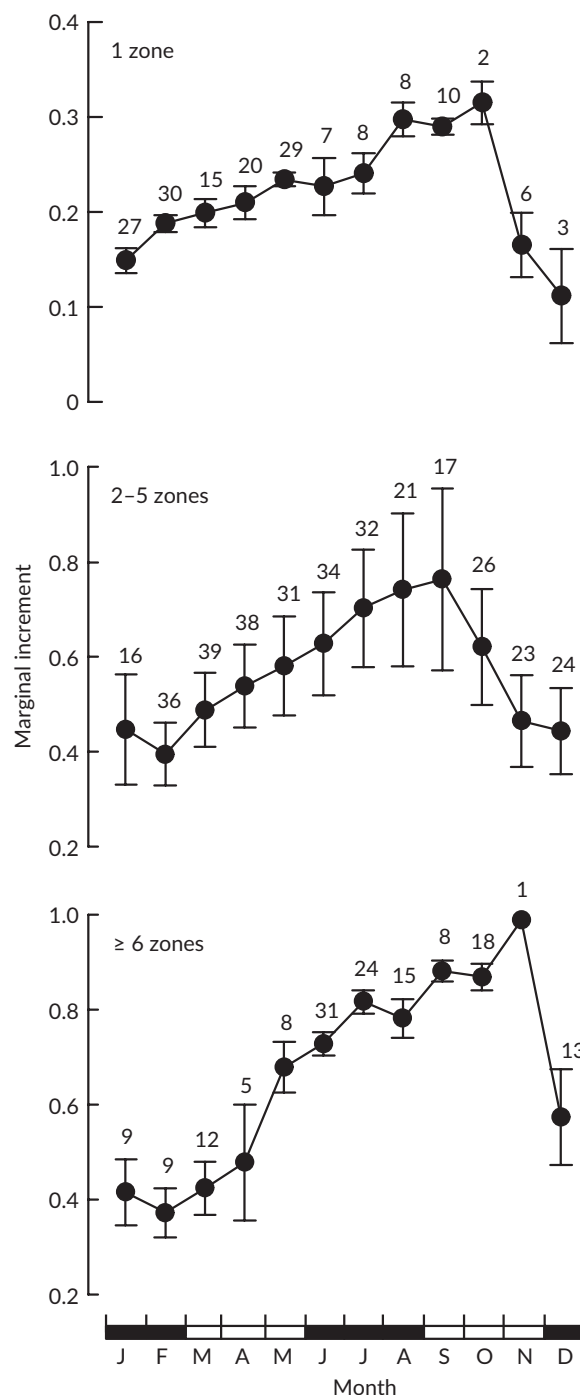


FIGURE 2 Monthly marginal increments (mean \pm SE) on sectioned sagittal otoliths of *Cheilodactylus rubrolabiatus* with different numbers of opaque zones. Sample sizes are given above each mean. On the x-axis, closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months

3.2 | Length and age composition and growth

ANCOVA showed that the relationships between M_T and both L_T and L_F did not differ significantly between sexes on each coast (both $P > 0.05$), but that the relationships for the combined sexes differed significantly between the south and lower west coasts ($P < 0.05$ and $P < 0.001$, respectively). The linear relationships between M_T and L_T and between M_T and L_F were: south coast $\ln M_T = 3.11(\ln L_T) - 11.93$ ($r^2 = 0.99$, $P < 0.001$, $n = 421$), $\ln M_T = 3.12(\ln L_F) - 11.71$ ($r^2 = 0.98$,

$P < 0.001$, $n = 421$); lower west coast $\ln M_T = 3.08(\ln L_T) - 11.76$ ($r^2 = 0.99$, $P < 0.001$, $n = 358$), $\ln M_T = 3.09(\ln L_F) - 11.57$ ($r^2 = 0.98$, $P < 0.001$, $n = 358$). The relationship between L_F and L_T did not differ significantly between the coasts ($P > 0.05$) and for both coasts was: $L_F = 0.92(L_T) + 1.51$ ($r^2 = 0.99$, $P < 0.001$, $n = 779$).

Female and male *C. rubrolabiatu*s caught on the south coast ranged in L_T from 169–540 and 152–571 mm, respectively, while those on the lower west coast ranged in L_T from 131–581 and 124–567 mm, respectively. The L_T composition of the *C. rubrolabiatu*s caught on each coast differed, with much larger modal sizes of 400–424 and 475–499 mm recorded for females and males, respectively, on the south coast compared with 300–324 and 275–299 mm, respectively, on the lower west coast (Figure 3a,b). The K-S test demonstrated that there was a significant difference between the L_T compositions of the corresponding sexes on the two coasts (both $P < 0.001$).

On the south coast, female and male *C. rubrolabiatu*s both ranged in age from <1–20 years of age, while on the lower west coast the ages ranged from <1–29 and <1–31 years, respectively. Of the fish sampled on the south coast, c. 90% of both the females and males were < 10 years of age, while on the lower west coast, a similar percentage of females and males were < 5 years old, with only very small numbers of individuals found in any of the older age classes on both coasts (Figure 3c,d).

The von Bertalanffy growth curves for females and males on the south coast and for females and males on the lower west coast

TABLE 1 Akaike Information Criterion values, for otoliths of *Cheilodactylus rubrolabiatu*s with marginal increments falling within the lower 30th percentile of values for each category of zone counts, determined by binomial circular distribution models fitted assuming no cycle, an annual cycle and a biannual cycle

South coast	1 Zone	2–5 Zones	≥ 6 Zones
No cycle	206	415	191
Annual cycle	168	335	128
Biannual cycle	198	418	187

Values in bold text are those that the associated models selected as best representing the data.

differed significantly ($P < 0.001$), with males on both coasts, on average, attaining a larger size at age. While the growth curves for females on the two coasts differed significantly ($P < 0.05$), this was not the case for males ($P > 0.05$). The difference in the L_T at age of females on the two coasts, however, as determined from their von Bertalanffy growth equations, was $\leq 5\%$ between ages 1 and 10 years, where most of the data lay. As these differences are small and growth curves will almost inevitably tend to differ significantly when based on large sample sizes (Cerrato, 1990), the differences are assumed, as in comparable cases (Coulson *et al.*, 2005, 2010, 2016), to be of little or no biological significance. Thus, the L_T at age for the corresponding sexes on the two coasts were combined to derive single growth curves for each sex (Figure 4). The von Bertalanffy growth curves provided an excellent fit to L_T at age of *C. rubrolabiatu*s over the age range

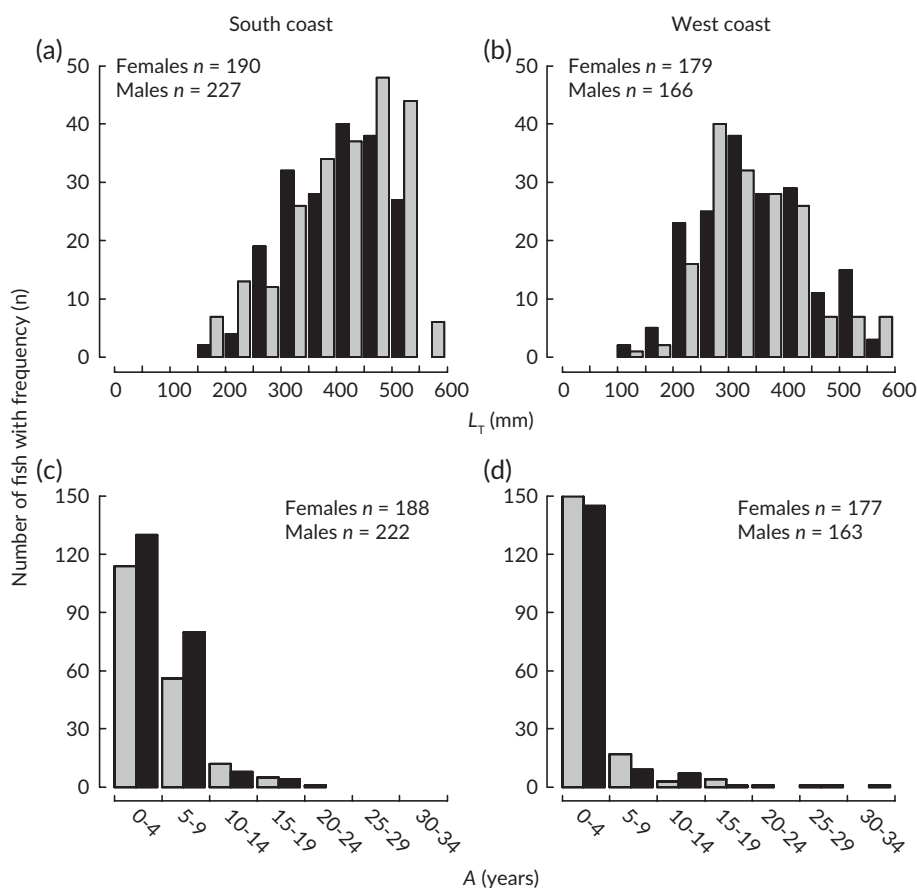


FIGURE 3 (a), (b) Total length (L_T)-frequency and (c), (d) age (a)-frequency distributions for female (○) and male (■) *Cheilodactylus rubrolabiatu*s on the south and lower west coasts of Western Australia. n = sample size

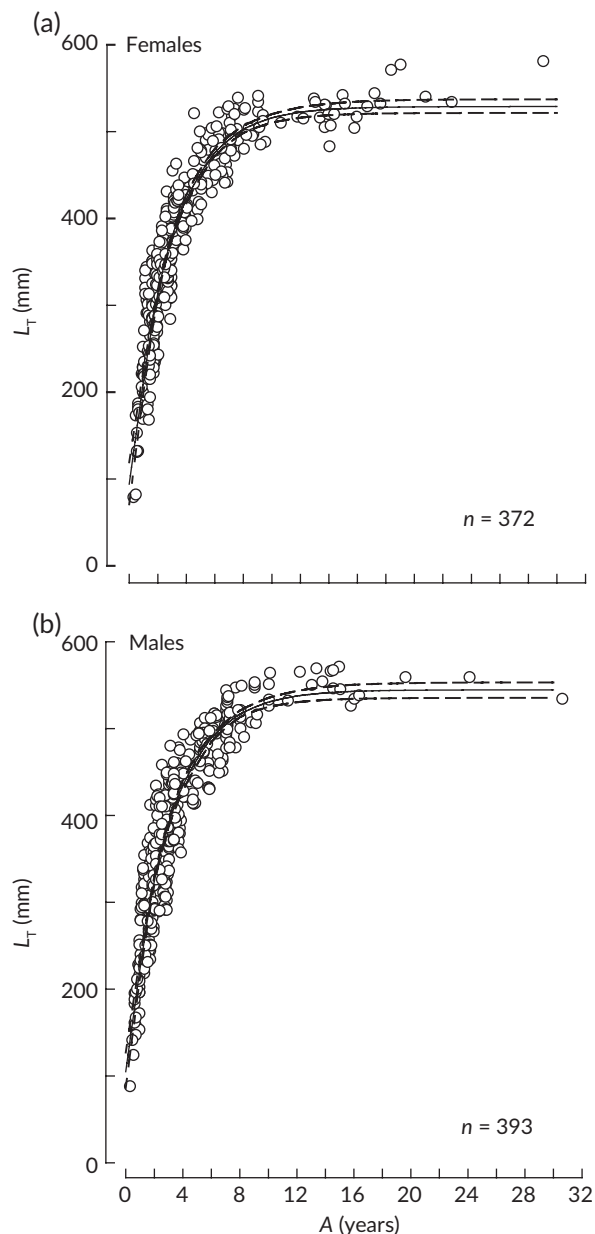


FIGURE 4 Von Bertalanffy growth curves (—), and their 95% confidence limits (---), fitted to the total lengths (L_T) at age (A) of (a) female and (b) male of *Cheilodactylus rubrolabiatus*, pooled from the south and lower west coasts of Western Australia

sampled, as demonstrated visually and by the high r^2 values (Table 2). Based on these growth curves, at ages 2, 5, 10, 15 and 20 years, females attained L_T of 313, 453, 516, 527 and 529 mm, respectively and males attained L_T of 325, 467, 531, 542 and 544 mm, respectively.

3.3 | Evidence of spawning time and duration and description of ovaries

The mean monthly I_{GS} for female *C. rubrolabiatus* \geq the L_{T50} on the south coast increased from 0.7 in January to a maximum of 1.5 in May, after which it declined to 0.7 in June and remained at this level or lower for the remainder of the year (Figure 5). The mean monthly I_{GS} for male *C. rubrolabiatus* \geq the L_{T50} on the south coast followed a

TABLE 2 The von Bertalanffy growth curve parameters and their upper and lower 95% CL, for the female and male *Cheilodactylus rubrolabiatus* derived from the total length (L_T) and fork length (L_F) at age of all aged individuals collected during the present study

	L_∞	k	t_0	r^2	n
Total length					
Females					
Estimate	532	0.32	−0.62	0.90	364
Upper 95% CL	543	0.35	−0.44		
Lower 95% CL	522	0.30	−0.79		
Males					
Estimate	549	0.31	−0.70	0.87	381
Upper 95% CL	562	0.35	−0.49		
Lower 95% CL	534	0.28	−0.91		
Fork length					
Females					
Estimate	487	0.35	−0.57	0.90	364
Upper 95% CL	495	0.32	−0.77		
Lower 95% CL	479	0.39	−0.37		
Males					
Estimate	502	0.34	−0.64	0.87	381
Upper 95% CL	512	0.38	−0.46		
Lower 95% CL	493	0.32	−0.80		

r^2 , Coefficient of determination; n, sample size.

similar trend to that for their females, albeit attaining a maximum of 0.5, 2 months earlier in March (Figure 5). On the lower west coast, the mean monthly I_{GS} for both females and males \geq the L_{T50} for each sex on that coast did not display an obvious trend, fluctuating from 0.4–0.9 and 0.1–0.3, respectively (Figure 5). The maximum values for females (0.9) and males (0.2) on the lower west coast, however, were attained in May and July respectively.

Female and male *C. rubrolabiatus* \geq the respective L_{T50} on both the south and lower west coasts possessed stage II gonads in most calendar months (Figure 5). Fish with stage III–IV gonads were present from February to June, while those few fish with stage V–VI gonads were present only in May or June. Females and males with stage VII–VIII gonads were present between May and November (Figure 5). The contrast between the presence of females and males with gonads at stages III–IV between February and July, those few fish with stage V–VI gonads in May and June and the increasing prevalence of fish with stage VII–VIII gonads from May to August support the conclusion that *C. rubrolabiatus* spawn predominantly between May to August. As 1 July represented the approximate mid-point of the spawning period for *C. rubrolabiatus*, this date was chosen as the birth date for those species.

During this study, only five females \geq their L_{T50} on each of the south and lower west coasts possessed stage V–VI ovaries during the proposed spawning period of May to August. The ovaries of these females were macroscopically characterised by their large size, taking up c. 60% of the body cavity, with yellow (yolk granule) oocytes easily visible through the thin, pink, translucent ovary wall and hydrated oocytes that flowed freely out the ovarian duct. During the same period and particularly on the south coast, there was a far greater number of females possessing stage VII–VIII ovaries, which were

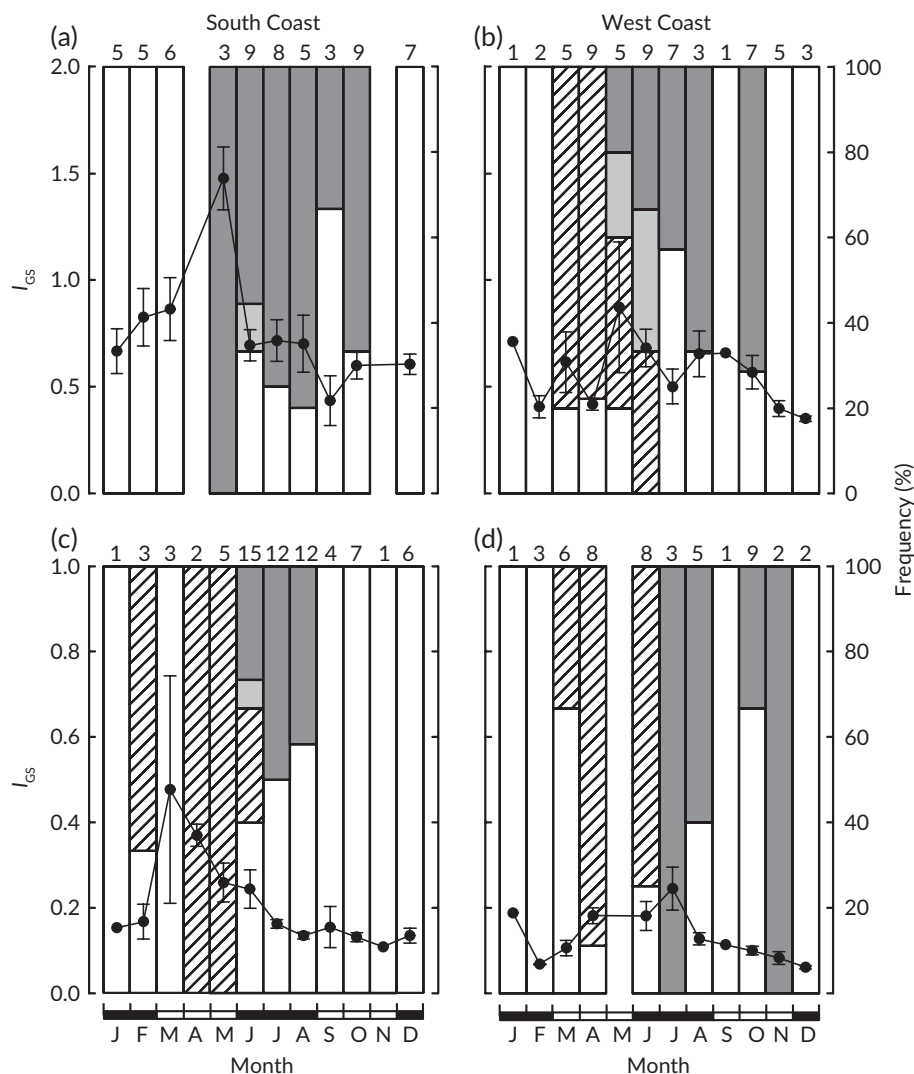


FIGURE 5 Monthly gonadosomatic indices (I_{GS} ; mean \pm SE) and the monthly percentage frequencies of occurrence of sequential stages in the gonadal development for a, b female and c, d male *Cheilodactylus rubrolabiatus*, greater than their respective total length at 50% maturity (L_{T50}), on a, (c) the south and b, d lower west coasts of Western Australia. Sample sizes are given above each month. □, Stage I–II; ▨, stage III–IV; ▤, stage V–VI; ■, stage VII–VIII. On the x-axis, closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months

characterised by being flaccid and possessing a thick, rubbery, opaque ovary wall.

3.4 | Lengths and ages at maturity

While all female *C. rubrolabiatus* < 400 mm, caught on the south coast during the spawning period, were immature, the prevalence of mature females increased to 15% and 44% in the 400–449 and 450–499 mm L_T classes, with all females ≥ 500 mm being mature (Figure 6). On the lower west coast, the prevalence of mature females increased from 8% to 36% in the 350–399 and 400–449 mm L_T classes, with all females ≥ 450 mm being mature (Figure 6). The L_{T50} for females was significantly ($P < 0.01$) longer on the south (472 mm) than the lower west coast (420 mm) (Table 3).

While all male *C. rubrolabiatus* < 350 mm, which were caught on the south and lower west coasts during the spawning period were immature, the prevalence of mature fish increased with increasing length class, such that all males on both coast ≥ 500 mm were mature (Figure 6). The L_{T50} for males was significantly ($P < 0.01$) longer on the

south (485 mm) than the lower west coast (412 mm; Table 3). While the L_{T50} for males was significantly ($P < 0.001$) longer than that of females on the south than west coast, it did not differ between the sexes on the lower west coast ($P > 0.05$).

During the spawning period, no female *C. rubrolabiatus* < 4 years old on the south coast possessed mature ovaries. The prevalence of females with such ovaries increased to 56% in the 5–9 years of age, with all females ≥ 10 years being mature (Figure 7). In contrast, on the lower west coast, although only 8% of females 1–4 years of age were mature, all females ≥ 5 years possessed mature ovaries. The A_{50} for females on the south and lower west coasts were 6.9 and 4.5 years of age, respectively (Table 3). The prevalence of male *C. rubrolabiatus* with mature testes on the south coast increased progressively from 27% at 1–4 years of age to 100% in the 15–19 year classes. Like their females, the prevalence of males with mature gonads on the lower west coast increased more rapidly with increasing age, such that all males ≥ 10 years were mature (Figure 7). The A_{50} for males on the south and lower west coast were 6.5 and 6.0 years, respectively (Table 3).

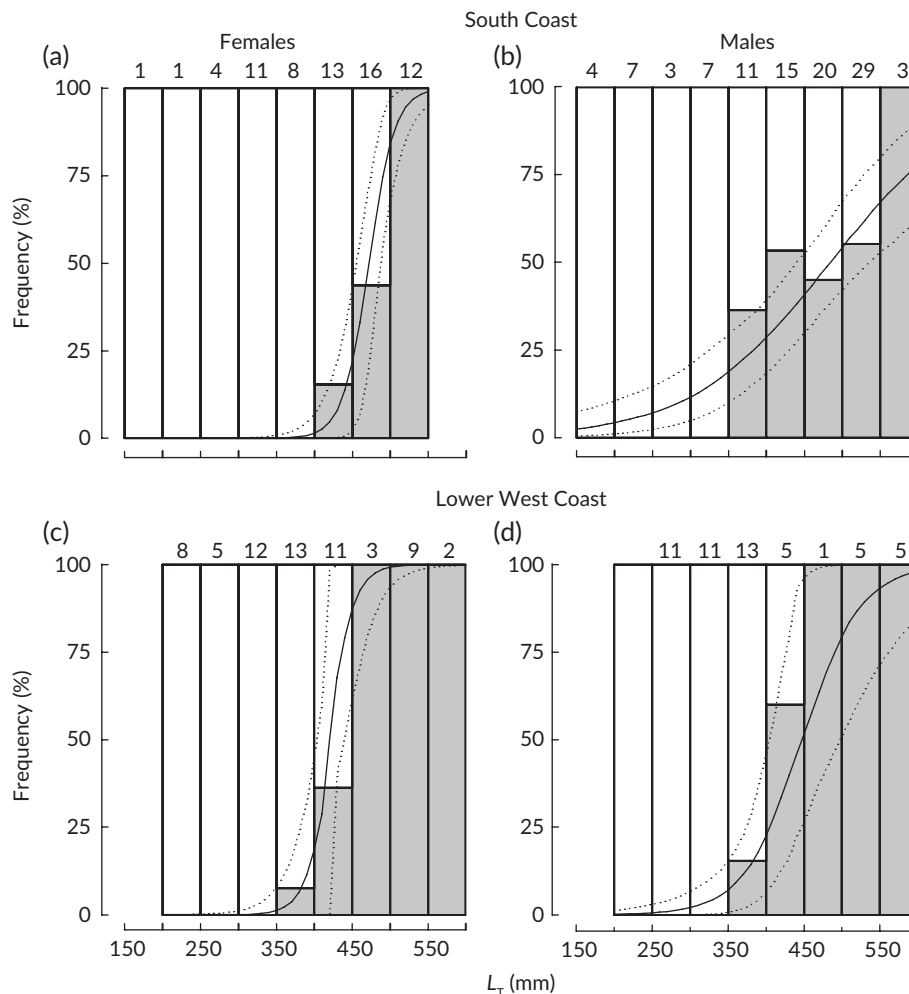


FIGURE 6 Percentage frequencies of occurrence of female and male *Cheilodactylus rubrolabiatus* with mature (stages III-VIII) gonads (■) in sequential 50 mm TL classes in samples obtained during the spawning period, i.e., May to August., 95% confidence limits. Sample size for each length class are shown above each column

3.5 | Life history characteristics of the Cheilodactylidae and Latridae

The maximum L_F for *Cheilodactylus* spp. range between 280 and 538 mm, which is very similar to *Nemadactylus* spp., except for *N. valenciennesi*, which attains greater maximum L_F , paralleling those for *Latris lineata* (Forster 1801) (Table 4). Most *Cheilodactylus* spp., *Nemadactylus* spp. and *L. lineata* exhibit moderate longevity of between 20 and 45 years, except *Cheilodactylus spectabilis* (Hutton 1872), which is extremely long-lived, attaining a maximum age of 97 years (Table 4).

The early growth of *Cheilodactylus* spp., *Nemadactylus* spp. and latrid species is very similar, being relatively rapid for the first 2–3 years of life (Figure 8). The difference in the growth patterns between species can largely be attributed to when an asymptote is reached. The growth of the females of *C. rubrolabiatus* and *Nemadactylus macropterus* (Forster 1801) from Tasmanian and New Zealand exhibit a very early and abrupt asymptote, at c. 3–4 years of age, while the growth of the female *Cheilodactylus fuscus* Castelnau 1879, *Cheilodactylus bergi* (Norman 1937), *C. spectabilis*, *Nemadactylus douglasii* (Hector 1875), *Nemadactylus valenciennesi* (Whitley 1937) asymptotes between c. 5–10 years of age. The growth of female *L. lineata* contrasts with the other cheilodactylids, attaining an asymptote much later at c. 20 years

of age. The males of the majority of species described above display a similar pattern of growth, although the growth of male *N. macropterus* from both Tasmanian and New Zealand asymptotes later than their females, at c. 10–15 years of age. In addition, the growth of male *N. valenciennesi* is remarkably similar to that the *L. lineata* and thus does not begin to asymptote until later in life, at an age > 15 years.

3.6 | Relationships between life history parameters of the Cheilodactylidae and Latridae

The estimated L_{F50} of female and most male, *Cheilodactylus* spp., *Nemadactylus* spp. and *L. lineata* all lie well within the range of L_{F50} predicted by their $L_{F\infty}$ (Figure 9a,b). However, the estimated L_{F50} of 484 and 412 mm for male *C. rubrolabiatus* from the south and lower west coasts, respectively, were above the upper boundary of the range of L_{F50} (125–402 mm for both) predicted by their $L_{F\infty}$ (Figure 9b). In addition, there is no noticeable trend in the relationships between L_{F50} and $L_{F\infty}$ for the females or males of the three genera to be distinctly different from one another. This is reflected in the percentage of the $L_{F\infty}$ that is the L_{F50} , which range widely from 45%–89% for females and males (Table 4).

TABLE 3 Estimates of the total length (L_T , mm), fork length (L_F , mm) and age (A, years) at which 50% and 95% of female and male *Cheilodactylus rubrolabiatulus* are mature, with their upper and lower 95% confidence limits

	L_{T50} (mm)	L_{T95} (mm)	L_{F50} (mm)	L_{F95} (mm)	A_{50} (years)	A_{95} (years)
South coast						
Females						
Estimate	472	522	436	474	6.9	9.9
Upper 95% CL	487	548	444	497	8.2	12.8
Lower 95% CL	455	494	423	456	5.7	7.3
Males						
Estimate	485	752	443	691	6.5	16.8
Upper 95% CL	535	944	495	871	9	24.9
Lower 95% CL	440	652	408	585	4.8	11.4
Lower west coast						
Females						
Estimate	420	467	387	428	4.3	5.5
Upper 95% CL	439	506	404	472	5	6.2
Lower 95% CL	404	417	374	392	4	5.5
Males						
Estimate	447	562	410	514	6	10.5
Upper 95% CL	497	673	458	617	7.8	14.9
Lower 95% CL	405	444	365	399	4.6	7.2

While the recorded A_{\max} s for female and male *N. douglasii*, *N. valenciennesi*, *L. lineata* and *C. rubrolabiatulus*, from both coasts and male *C. bergi* lie within the range of ages predicted by their respective A_{50} (Figure 9c), the recorded A_{\max} for female (30 years) and male (41 years) *N. macropterus* lie well above the upper boundary of this range predicted from their A_{50} . In the most extreme case, the maximum age of 94 years recorded for female *C. spectabilis* is far above the range of c. 6–37 years predicted from its A_{50} of 4.5 years (Murphy & Lyle, 1999). As a percentage of their maximum age, the A_{50} range from 5% to 21% for the females and males of all species, except female and male *C. rubrolabiatulus* from the south coast whose A_{50} represent 35% and 34%, respectively, of their maximum ages (Table 4).

The $M:k$ for female and male *Cheilodactylus* spp. range from 0.45–0.65 ($\bar{x} = 0.48$) and 0.45–0.71 ($\bar{x} = 0.63$), respectively, while those for *Nemadactylus* spp. range from 0.42–0.76 ($\bar{x} = 0.55$) and 0.24–1.00 ($\bar{x} = 0.57$), respectively. In comparison with other *Cheilodactylus* spp. and *Nemadactylus* spp., the $M:k$ for female and male *L. lineata* and *C. fuscus* are higher than what would be expected for species that attain ages ≥ 30 years. In the studies of these two species, very few small, young fish were obtained (Lowry, 2003; Tracey & Lyle, 2005). As a result, the VBGE parameter t_0 is highly negative, which results in a shallow growth curve suggesting slower growth as indicated by low values of k (Table 4).

4 | DISCUSSION

4.1 | Length and age compositions and growth

The length and, to a lesser extent, age compositions of *C. rubrolabiatulus* collected from the south and lower west coasts of Western Australia

demonstrate that the sampled population on the former coast consists of greater numbers of larger and older fish than populations on the latter coast. As spear fishing was employed to collect samples of *C. rubrolabiatulus* from both coasts and was capable of sampling the full size range of individuals encountered, the differences in the length composition are proposed to be a result of differences in the habitat in each region. In many instances, there are steep rocky reefs along the shoreline of the south coast, often dropping-off quickly to depths of 10–20 m, with large expanses of open sand separating these reefs (Kendrick *et al.*, 2005a). Non-preferred sand habitat can act as a natural boundary to the movements of reef-associated species (Chapman & Kramer, 2000; Kramer & Chapman, 1999), including the co-occurring labrid *Achoerodus gouldii* (Richardson 1843) (Bryars *et al.*, 2012) and its congener *Achoerodus viridis* (Steindachner 1866) (Lee *et al.* 2014), as well as other labrids and serranids (Barrett 1995; Farmer & Ault, 2011). While wide sand expanses may be preventing *C. rubrolabiatulus* from moving to deeper reefs, further offshore, the wide depth range on reefs along shorelines on the south coast (Kendrick *et al.*, 2005b) may provide adequate habitat for all life cycle stages that, in shallower waters, would require a fish to move further offshore to encounter.

Coastal marine waters along the lower west coast of Western Australia, in contrast, are characterised by a shallow depth gradient and a series of fringing reefs, connecting inshore waters and islands with reefs in deeper offshore waters (Fairclough *et al.*, 2011). This connection probably facilitates the offshore movement of *C. rubrolabiatulus*, as it does for the King George whiting *Sillaginodes punctatus* (Cuvier 1829) and West Australian dhufish *Glaucosoma hebraicum* Richardson 1845 in this region (Hesp, *et al.* 2002; Hyndes *et al.* 1998) and teleosts in other temperate regions (Gillanders, 1997; Gillanders & Kingsford, 1998; Shepherd & Brook, 2007). The ability of

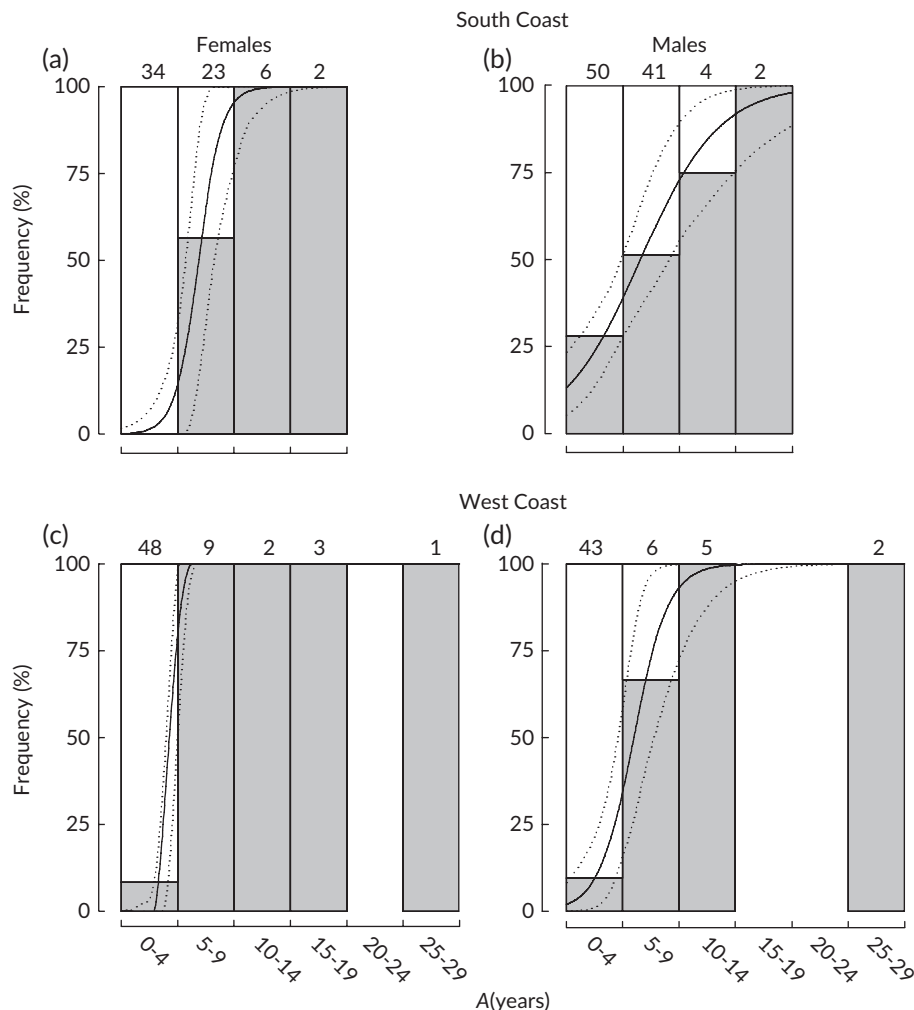


FIGURE 7 Percentage frequencies of occurrence of female and male *Cheilodactylus rubrolabiatus* with mature (stages III-VIII) gonads (■) in sequential 5 year age classes in samples obtained during the spawning period, i.e., May to August. -----, 95% confidence limits. Sample size for each length class are shown above each column

C. rubrolabiatus to move further offshore, to deeper, less accessible reefs on the lower west coast may have contributed to the underrepresentation of larger and older individuals in samples collected in this study. Indeed, one of the largest (559 mm L_T) and the third oldest (25 years), *C. rubrolabiatus* collected from the lower west coast was caught in waters near Rottne Island (32° 00' S, 115° 30' E), approximately 18 km from those inshore reefs that were visited during regular sampling trips. The apparent offshore movement of *C. rubrolabiatus* in waters on the lower west coast reflects that observed for the closely-related *C. spectabilis* in waters off north-eastern New Zealand, where the mean size of that species was related to water depth, with small individuals being restricted to shallow waters (Leum & Choat, 1980; McCormick, 1989). Likewise, another cheilodactylid, *N. valenciennesi* move further offshore with increasing size (Coulson *et al.*, 2010) and size-structuring by depth is believed to reflect the offshore movement of *L. lineata* as they grow and mature (Tracy & Lyle, 2005).

The maximum ages of 29 and 30 years recorded for female and male *C. rubrolabiatus* in the present study, respectively, are similar to maximum ages recorded for other *Cheilodactylus* spp., *Nemadactylus* spp. and *L. lineata*, which typically range between 19 and 43 years

(Table 4). Despite other cheilodactylids being targeted by commercial and recreational fishers, *C. rubrolabiatus* is not rated highly as a food fish and is rarely caught, if ever. Thus, the maximum ages determined in the current study reflect the maximum age of an unfished population of this species. It is therefore very surprising that despite attaining maximum L_F greater than, or similar to, that of two congeners, *C. spectabilis* and *C. fuscus*, which are commercially and recreationally exploited (Lowry & Suthers, 2004; Murphy & Lyle, 1999; Ziegler *et al.*, 2005), the maximum ages of *C. rubrolabiatus* are c. one third of that of *C. spectabilis* and 10 years lower than that recorded for male *C. fuscus* (Table 4). Coulson *et al.* (2010) suggested that the longer life spans of the latter two species, in conjunction with limited body growth throughout a long period of their lives, represent the results of selection pressures that ensure these species have the opportunity to spawn over many years. Although female and male *C. rubrolabiatus* also exhibit limited growth over a long period of their lives (c. 20–25 years), on average, they grow to a larger size prior to maturity. In fact, the L_{F50} for female and male *C. rubrolabiatus* on the south and lower west coasts are $\geq 75\%$ of the $L_{F\infty}$, the highest percentage of any of the *Cheilodactylus* or *Nemadactylus* species (Table 4). This may represent selection pressures of pair spawning and the need, particularly

TABLE 4 von Bertalanffy growth parameters ($L_{F\infty}$, k and t_0), instantaneous natural mortality rates (M), maximum fork length (L_{Fmax}), maximum age (A_{max}), fork length and ages at first maturity (L_{F50} ; A_{50}), the percentage of fork length ($\%L_{F\infty}$) and maximum age ($\%A_{max}$) that is represented by the L_{F50} and A_{50} , respectively, and the ratio of $M:k$ for members of the Cheilodactylidae and Latridae for which there are substantial data

	$L_{F\infty}$ (mm)	k (year ⁻¹)	t_0 (years)	M (year ⁻¹)	L_{Fmax} (mm)	A_{max} (mm)	L_{F50} (mm)	A_{50} (years)	$\%L_{F\infty}$	$\%A_{max}$ (years)	$M:k$
<i>C. rubriolabiatus</i> ¹											
F	487	0.35	-0.57	0.21 ^S ; 0.14 ^W	499 ^S ; 538 ^W	20 ^S ; 29 ^W	436 ^S ; 387 ^W	6.5 ^S ; 6.0 ^W	89 ^S ; 79 ^W	35 ^S ; 19 ^W	0.65 ^S ; 0.45 ^W
M	502	0.34	-0.64	0.22 ^S ; 0.14 ^W	533 ^S ; 521 ^W	19 ^S ; 30 ^W	443 ^S ; 410 ^W	6.8 ^S ; 4.3 ^W	88 ^S ; 81 ^W	34 ^S ; 20 ^W	0.71 ^S ; 0.45 ^W
<i>C. fuscus</i> ²											
F	376	0.22	-3.60	0.12	460	34					0.55
M	454	0.13	-5.39	0.10	450	40					0.80
<i>C. spectabilis</i> ^{a,3,4}											
F				0.04	496	94	324	4.5		5	
M				0.04	552	97					
<i>N. valciennesi</i> ⁵											
F	696	0.29	-0.36	0.22	846	19	400	3	48	16	0.76
M	839	0.22	-0.52	0.22	867	19	500	3	51	16	1.00
<i>N. macropterus</i> ^{a,6,7} (Tas)											
F	384	0.33	0.40	0.14	455	30	270	3	70	10	0.42
M	362	0.42	0.15	0.10	423	41	250	3	69	7	0.24
<i>N. macropterus</i> ^{a,8} (NZ)											
F	461	0.22	-0.69	0.09	510	44					0.43
M	432	0.25	-0.55	0.11	470	39					0.43
<i>N. douglasii</i> ^{c,9}											
F	331	0.35	-0.44	0.21	470	20	236	3	71	15	0.60
M	397	0.32	-0.34	0.20	524	21	236	2.5	59	12	0.62
<i>N. bergi</i> ^{10,11}											
F	347	0.33	-0.16	0.16		26	237	~2.6	68	10	0.49
M	320	0.40	0.00	0.22		19	213	~2.6	67	14	0.55
<i>Latris lineata</i> ^{b,12,13}											
F	773	0.15	-1.46	0.09	950	43	543	6.8	70	16	0.64
M	773	0.15	-1.46	0.14	815	29	529	6.2	68	21	0.96

¹Present study, ²Lowry (2003), ³Ewing et al. (2007), ⁴Murphy and Lyle (1999), ⁵Coulson et al., (2010), ⁶Jordan (1998), ⁷Jordan (2001), ⁸Stevenson and Horn (2004), ⁹Stewart and Hughes (2009), ¹⁰Wöhler (1997a), ¹¹Wöhler (1997b), ¹²Tracey and Lyle (2005), ¹³Tracey et al. (2007).

^aValues the lower west and south coasts of Western Australia.

^bSchnute growth curve used as it provided a better fit than the VBGE (Ewing et al., 2007). Biological details for *N. macropterus* from New Zealand waters. Biological details for *N. macropterus* from Tasmanian waters.

^cThe von Bertalanffy growth parameters for *L. lineata* were determined for females and males combined.

^dEstimates of L_{F50} estimates for *N. douglasii* were determined for females and males combined.

in males, to attain a large size in order to actively compete for mates (see below).

4.2 | Reproduction and habitat

Despite collecting a wide size range of *C. rubrolabiatu*s during the spawning period and observing numerous females with stage VII–VIII ovaries during this time, very few females with stage V–VI ovaries were encountered. Initially, it was thought that the lack of females and males with stage VII–VIII gonads on the south coast may be due to an offshore migration, similar to that observed in the confamiliar *N. valenciennesi* and the labrid *A. gouldii* on the same coast (Coulson *et al.*, 2009, 2010). However, very few females with prespawning–spawning ovaries were likewise encountered on the lower west coast.

McCormick (1989) observed that, over the duration of a day during the spawning period, the density of ripe female *C. spectabilis* peaked at dusk, which is similar to that observed in other temperate and tropical reef fish species (Colin, 2012; Sadovy, 1996). It is thus relevant that, sampling for *C. rubrolabiatu*s by spear fishing was conducted largely early in the day, which may have precluded the collection of prespawning–spawning individuals. The presence of large numbers of females with VII–VIII ovaries, characterised macroscopically by thick, rubbery walls as a result of expansion and contraction of the ovary (Lowerre-Barbieri *et al.*, 2011), in samples collected in the morning during the spawning period, suggests that these females may have recently spawned, perhaps the prior evening.

The small size of the gonads of males collected during the spawning period indicates that *C. rubrolabiatu*s spawns in pairs or very small groups. This is consistent with *C. spectabilis* in north-eastern New Zealand and Tasmania for which the gonad mass of males is only a fraction of that for their females (McCormick, 1989; Murphy and Lyle, 1999). Underwater observations by McCormick (1989) indicated that male *C. spectabilis* occupy deeper habitats on the reef edge during the spawning period, defending these sites from other males and chasing females into sites, thereby presumably gaining exclusivity to visiting females. The ability to spawn exclusively and at close proximity, with a female, reduces the need for large quantities of sperm and thus large gonads. This type of spawning system parallels that of temperate serranids (French *et al.*, 2014; Moore *et al.*, 2007), labrids (Coulson *et al.*, 2009; Cossington *et al.*, 2010) and other species such as pantacerotids (Coulson *et al.*, 2016) that spawn in pairs or small groups and whose males possess very small gonads during the spawning period. However, this spawning system contrasts with that for confamiliars *N. valenciennesi* and *N. macropterus* and the closely-related *L. lineata*, which occupy deeper, more offshore waters and spawn in large groups or schools and whose spawning males possess gonads that are only slightly smaller than those of their females (Coulson *et al.*, 2010; Jordan, 1998; Tracey *et al.*, 2007).

4.3 | Environmental and social influences on the biology of *Cheilodactylus rubrolabiatu*s

In the current study, the growth of female *C. rubrolabiatu*s did not differ between the south and lower west coasts and the difference in the growth of males on these two coasts was negligible, paralleling

the patterns in growth exhibited by the confamiliar *N. valenciennesi* collected from the same regions (Coulson *et al.*, 2010). These growth patterns run contrary to premises of the TSR, whereby individuals in the cooler waters of the south coast should grow slower than those in warmer waters of the lower west coast (Angilletta *et al.*, 2004; Atkinson, 1994; Brown *et al.*, 2004; Charnov & Gillooly, 2004), as has been demonstrated for other temperate species (Cowen, 1990; Hughes *et al.*, 2017; Lek *et al.*, 2012; Trip *et al.*, 2014). Further counter to the predictions of TSR, the maximum age of female and male *C. rubrolabiatu*s on the cooler south coast is less than that for the corresponding sex on the warmer lower west coast. However, the maturation of females and males on the south coast occurs at a greater length and age, than the corresponding sexes on the lower west coast, as would be expected based on the TSR.

Thus, it appears that although differences in environmental conditions on the two coasts may not be sufficient to influence the growth of *C. rubrolabiatu*s, other factors, such as social stimuli, may be influencing the timing of maturation. As mentioned earlier, the discontinuity of habitat on the south coast means that *C. rubrolabiatu*s of all sizes are likely to be concentrated to the same reef. Thus, in this

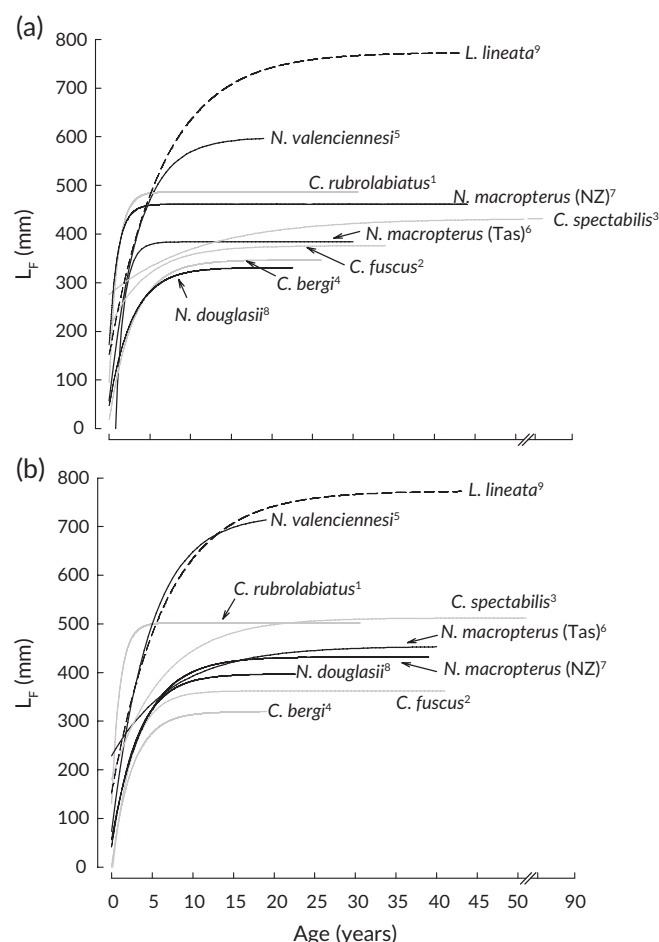


FIGURE 8 Growth curves for a females and b males of Cheilodactylid and Latrid species for which fork length (L_F)-at-age data are available. von Bertalanffy growth curves were used for each species except for *C. spectabilis* for which the Schnute growth curve was used. ¹Present study, ²Lowry (2003), ³Ewing *et al.*, (2007), ⁴Wöhler (1997a), ⁵Coulson *et al.*, (2010), ⁶Jordan (2001), ⁷Stevenson and Horn (2004), ⁸Stewart and Hughes (2009), ⁹Tracey and Lyle (2005)

region, maturation, particularly in males, may be delayed until they are of a large enough size capable of competing successfully for mates and habitat, which is not required of males on the lower west coast where the greater availability of habitat diffuses competition.

4.4 | Comparison of life history characteristics of the Cheilodactylidae and Latridae

The results of the analysis of the relationship between the L_{F50} and $L_{F\infty}$ for female and male *Cheilodactylus* spp., *Nemadactylus* spp. and latrid species (Figure 9a,b) are consistent with the fact that fish that attain larger sizes typically mature at a greater length (Charnov & Berigan, 1991; Froese & Binohlan, 2000). As *L. lineata* attains the largest size, this species matures at the length greater than most *Nemadactylus* spp. and all *Cheilodactylus* spp., which attain smaller sizes and thus mature at smaller lengths. However, the relationship between A_{max} and A_{50} for those species does not exhibit a clear trend, with maturation occurring either at 2–3 or 6–7 years of age, irrespective of what maximum age they attain (Figure 9b and Table 4).

The $M:k$ for female and male *Cheilodactylus* spp. and *Nemadactylus* spp. were very similar, as would be expected of confamilials (Beverton, 1992), but are far lower than the 1.5 defined by Jensen (1996) as the average for fish populations. A recent meta-analysis by Prince *et al.* (2014) demonstrated that groups of a wide range of marine taxa, from large marine mammals to small crustaceans, display similar life history strategies. The results for *Cheilodactylus* spp. and *Nemadactylus* spp. indicate that they fall into the type II group of species (i.e., $M:k < 1.0$ and indeterminate growth), defined by Prince *et al.* (2014), thus paralleling several tropical lutjanid species, but also, surprisingly, the deep-water and extremely long-lived *H. atlanticus*. Type II species display initial rapid growth, maturity at a size close to their asymptotic length and exhibit little or no adult growth and are typified by an accumulation of adults in the population that live for an extended period (Hordyk *et al.*, 2015; Prince *et al.*, 2014). In terms of life-history strategies, *Cheilodactylus* spp. and *Nemadactylus* spp., and other type II group species, can be classed as *K*-strategists (Pianka, 1970), or periodic and equilibrium strategists (King & McFarlane, 2003). This type of life-history strategy is often associated with species that exhibit highly variable recruitment, as a result of oceanographic variability, to ensure that adults contribute to spawning events over many years, thus hopefully encountering favourable conditions in some of those years (Longhurst, 2002; Winemiller, 2005).

Burridge and Smolenski (2004) previously suggested that Greenwood's (1995) proposal to reassign *Nemadactylus* spp. to the closely-related Latridae is not appropriate based on morphological characteristics. This is confirmed by the current study, as the growth of all *Nemadactylus* spp., except *N. valenciensi*, more closely resembles that of *Cheilodactylus* spp., rather than that of *L. lineata* and *L. ciliaris* (Figure 8). In addition, the results of the relationships between L_{F50} and $L_{F\infty}$ and between maximum age and A_{50} , and $M:k$, there would appear little evidence to suggest that *Cheilodactylus* spp., *Nemadactylus* spp. and *Latris* spp. are biologically very different from one another. These results, combined with the fact that Latridae and non-South African *Cheilodactylus* spp. are not genetically distinct (Burridge & Smolenski, 2004), may provide further justification for the

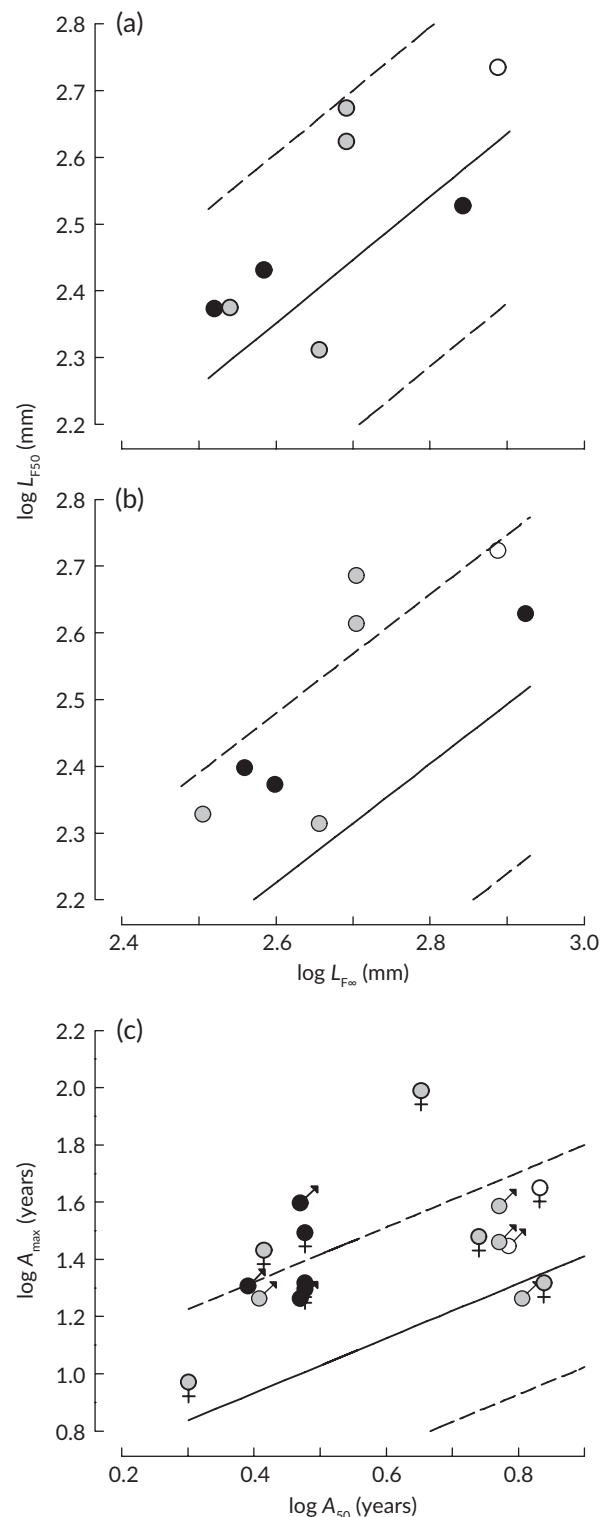


FIGURE 9 The relationship between the fork length at maturity (L_{F50}) estimates and asymptotic length ($L_{F\infty}$) for a females and b males. c The relationship between maximum age (A_{max}) and age at maturity (A_{50}) estimates for female and male *Cheilodactylus* spp. (●), *Nemadactylus* spp. (○) and latrid (○) species for which there are substantial data. The regression (—) and the 95% CI (---) for the relationship between those variables for 265 species developed by Froese and Binohlan, 2000 are shown

amalgamation of these three genera into a single family. Further work to determine the biological characteristics of the South African *Cheilodactylus* species, *Cheilodactylus fasciatus* and *Cheilodactylus pixi* Smith

1980, as well as *Acantholatris* spp., which are synonymous with the *Nemadactylus* genus (Burrige, 1999), would provide further clarity on this issue.

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CONFLICTS OF INTEREST

The author declares that there are no conflict of interest.

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