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Life cycle characteristics of the Blue Morwong *Nemadactylus valenciennesi*, compared with those of other species of Cheilodactylidae

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10 **Running head:** Life history characteristics of a large species of morwong

15

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Abstract

25 The distribution, length and age compositions, growth and the length and age at maturity
of the reef fish *Nemadactylus valenciennesi* in south-western Australian waters have been
determined. Comparisons between these data and those for other cheilodactylids demonstrate
that the life history characteristics in this small family differ markedly. The maximum age (21
years) of *N. valenciennesi* (maximum total length = 984 mm) is far less than those of the much
30 smaller *Cheilodactylus fuscus*, *Nemadactylus macropterus* (both ~ 40 years) and *Cheilodactylus*
spectabilis (97 years). Yet *N. valenciennesi*, *N. macropterus* and *C. spectabilis* mature at a
similar young age (3-7 years). While, on the basis of data for other species, all three species
mature at lengths consistent with their asymptotic lengths, the last two species mature at a far
earlier age than would be predicted from their long spans. The relatively very early attainment of
35 maturity by *N. macropterus* and *C. spectabilis* may reflect selection pressures associated with
particularly high mortality among younger fish and/or constrained growth of adults, while their
far longer life spans could reflect selection pressures in response to variable recruitment in the
past and/or compensation for limited annual reproductive output due to very constrained growth
of adults.

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Additional keywords: Growth, longevity, spawning, maturity, regional differences, confamilial
45 comparisons

Introduction

The Cheilodactylidae (morwongs) is thus named because its 22 species possess large fleshy lips and enlarged pectoral fins in which some of the lower fin rays are extended (Lowry and Cappo 1999; Allen *et al.* 2006). The members of this family inhabit rocky reefs in subtropical and temperate regions and are most speciose in the temperate waters of Australia, Japan and southern Africa (Allen *et al.* 2006; Nelson 2006). Detailed information on the length and age compositions, growth and reproductive biology of cheilodactylids have been provided by Murphy and Lyle (1999), Ewing *et al.* (2007) and Zeigler *et al.* (2007) for the banded morwong *Cheilodactylus spectabilis*, by McCormick (1989a, 1989b) for the red morwong *Cheilodactylus fuscus* and by Jordan (2001a) and Lowry (2003) for the jackass morwong *Nemadactylus macropterus*, which are all commercially and/or recreationally important. These three species attain similar maximum fork lengths (FL), with those of their females, for example, ranging only from ~ 460 to 500 mm.

Although the above three species are all relatively long-lived, i.e. ≥ 30 years, the maximum age attained by *C. spectabilis* is well over twice that recorded for either sex of *N. macropterus* and *C. fuscus* (Jordan 2001a; Lowry *et al.* 2003; Ewing *et al.* 2007). Despite the marked differences in their maximum ages, *N. macropterus* and *C. spectabilis* both exhibit a markedly asymptotic pattern of growth and reach maturity relatively early in life (Jordan 1998; Zeigler *et al.* 2007). The larvae of cheilodactylids settle at a relatively large size after spending many months in the plankton, during which they can be transported long distances from their spawning areas (Vooren 1972; Lowry and Cappo 1999; Bruce *et al.* 2001). The juveniles of *N. macropterus* are concentrated on the inner to mid-shelf, whereas its adults are found on the outer shelf (Jordan 2001b).

70 The blue morwong *Nemadactylus valenciennesi* lives over rocky reefs in the waters of southern Australia (Hutchins and Thompson 1983; Allen *et al.* 2006). As the maximum recorded total length (TL) of *N. valenciennesi* is nearly 1 m (Gomon *et al.* 2008), this cheilodactylid reaches a far larger size than *N. macropterus*, *C. spectabilis*, and *C. fuscus*. Although, in Western Australia (W.A.), *N. valenciennesi* is found on the reefs of both the southern and lower west
75 coasts of W.A., it is largely restricted to deeper reefs on the latter coast (Hutchins and Thompson 1983). On the south coast of W.A., *N. valenciennesi* is the greatest contributor to the biomass of the catches taken by its Demersal Gillnet and Longline Fishery (McAuley and Simpfendorfer 2003) and one of the species most frequently retained by recreational fishers (Johnson and Lai 2006). The substantial catches taken by both fishing sectors demonstrate that *N. valenciennesi*
80 must play an important role in the ecology of reef ecosystems in southern Australia and account for the proposal that this species be used as an indicator of the quality of recreational fishing on the south coast of W.A. (Anon 2005). Despite the ecological, commercial and recreational importance of *N. valenciennesi*, little is known about the biology of this cheilodactylid.

 This study was aimed at providing data on the length and age compositions, growth,
85 spawning period and length and age at maturity of *N. valenciennesi* in south-western Australian waters to address the following questions. 1) Is the far larger size attained by *N. valenciennesi* than by the congeneric *N. macropterus* and other well-studied cheilodactylids (*C. spectabilis* and *C. fuscus*) accompanied by a greater longevity and the attainment of maturity at a larger size and older age? 2) Does the growth of both sexes of *N. valenciennesi* show the same remarkable
90 tendency to converge to an asymptote so early in life as the above three species of cheilodactylid? 3) Does *N. valenciennesi* undergo the same type of size-related movement into deeper waters as *N. macropterus* and can water movements during its protracted larval phase

account for differences in the distributions of this species on the south and lower west coasts of W.A.?

95 When the data collected for *N. valenciennesi* were compared with those recorded for other species of cheilodactylid, it became apparent that, in particular, the relationships between age at maturity and longevity differed markedly among the members of this small family. This led us to use existing empirical equations relating various life cycle parameters across a broad range of fish taxa (Freose and Binohlan 2000) to explore which cheilodactylid species diverge
100 from the typical pattern found among fish species.

Materials and methods

Sampling regime and environmental measurements

Nemadactylus valenciennesi was collected between March 2004 and October 2007 from coastal
105 waters of W.A. between ~ 35°S, 118°E and ~ 34°S, 122°E on the south coast and from ~ 32°S, 116°E on the lower west coast. Nearshore waters on the south coast were sampled by spear fishing over and around reefs in shallow (< 20 m) inshore waters along the mainland and around islands. *Nemadactylus valenciennesi* was never observed during extensive sampling for other species in reef habitats in nearshore waters on the lower west coast during the same period as the
110 south coast was sampled. Fish in offshore waters were obtained from catches taken on both coasts either by commercial gillnet fishers, using nets with a mesh range of 165-178 mm in water depths of ~ 20-100 m, or by recreational fishers in water depths of ~ 20-50 m. The fish supplied by recreational fishers and some of those by commercial fishers had been filleted but still contained their gonads, while the remaining fish from commercial fishers were filleted and
115 eviscerated, i.e. contained no gonads. Spear fishing was undertaken in October 2004 and

typically monthly or bimonthly between May 2005 and November 2006. Samples were collected from commercial gillnetters in May, June, September and October, 2004, all months in 2005 except April and typically at monthly or bimonthly intervals between January 2006 and January 2007. Samples were supplied by recreational fishers in most months between March 2004 and
120 October 2007.

Inshore surface water temperatures at Albany (~ 35°S, 118°E) and Esperance (~ 34°S, 122°E) on the south coast, as recorded by the Department of Fisheries, Western Australia at intervals in 1994-2006, were pooled and used to calculate the mean and its standard error for each calendar month. The mean monthly offshore surface temperatures in waters off Albany,
125 Esperance and Rottnest Island (~ 32°S, 116°E) on the lower west coast in 2004-2006 were derived from water temperatures obtained from a combination of satellite imagery and by shipping and drifting buoys (see Reynolds and Smith (1994) for methodology).

Length and weight measurements,

130 A total of 1872 *N. valenciennesi* was collected for this study, of which 330 were intact, 655 were filleted but contained gonads and 887 were filleted and eviscerated. All fish except those in the last category could be sexed. The total length (TL) and gonad weight (GW) of each intact fish and each filleted fish with gonads were recorded to the nearest 1 mm and 0.01g, respectively. The TLs of eviscerated fish and the fork length (FL) of fish in subsamples of 275 females and
135 368 males, comprising both intact and filleted fish with gonads, were also recorded to the nearest mm.

As ANCOVA, employing FL as the dependent variable, TL as the independent variable and sex as the fixed factor, showed that the relationships between FL and TL for females and

males were not significantly different ($P > 0.05$), the data sets for FL and TL for both sexes were
140 pooled. The linear relationship between FL and TL is given by the equation:

$$FL = 1.010(TL) - 0.219 \quad (r^2 = 0.996, P < 0.001, n = 643).$$

This equation enabled the TLs recorded during the present study to be expressed as FLs and thus
facilitated comparisons with the FLs recorded in studies of other cheilodactylids (*e.g.* Murphy
and Lyle 1999; Jordan 2001*a*; Lowry 2003; Ewing *et al.* 2007).

145 All 1872 fish were used to construct the length-frequency histogram shown in the
Results. All fish except those 282 individuals which the commercial fisher wished to retain intact
and the small number of these in which the opaque zones in the otoliths were poorly defined
were employed to produce the age-frequency histogram and marginal increment figure. Growth
curves, gonadal weight and relationships between maturity and length and age used data derived
150 from fish that were either fully intact or had been filleted but still contained gonads.

Age determination and growth

A preliminary examination of whole and sectioned otoliths from a wide length range of
N. valenciennesi showed that the opaque zones were more readily detectable in sectioned than
155 whole otoliths and therefore led to higher counts of those zones. All otoliths were thus sectioned.
One sagittal otolith from each fish was embedded in clear epoxy resin and cut transversely
through its primordium into ~ 0.3-mm sections employing a low-speed diamond saw (Isomet
Buehler). The sections were polished on wet and dry carborundum paper (grade 1200) and
mounted on microscope slides using DePeX mounting adhesive and a cover slip. A digital
160 microscopic image of each sectioned otolith and of its peripheral region at a higher magnification
were used, respectively, for counting opaque zones and measuring the distances required for

marginal increment analysis (see below). These images were taken using transmitted light and employing an Olympus DP70 camera mounted on an Olympus BX51 compound microscope. All images were archived in Leica Image Manager 1000 (Leica Microsystems Ltd 2001), which
165 enabled the opaque zones to be marked and counted accurately and the distances required for marginal increment analysis (see below) to be measured precisely. All counts and measurements were made on the ventral side of the otolith.

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
170 otolith periphery, were used to validate that a single opaque zone is formed annually in the otoliths of *N. valenciennesi*. The marginal increment 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
175 and along the same perpendicular axis to the opaque zones.

An autocorrelation approach, similar to that employed by Vilizzi and Walker (1999), was used to validate that the growth zones in otoliths of *N. valenciennesi* are formed annually. In brief, autocorrelation coefficients were calculated from the mean monthly marginal increments for each year and month, using lags ranging from 0 to 24 months. Student t-tests were used to
180 determine whether the correlation coefficient for each lag (in months) differed significantly from 0 (Zar 1999).

The number of opaque zones in each sectioned otolith was counted by the first author on two occasions, and on a third occasion when the first two counts were not the same. In the latter situation, the third count was always the same as one of the first two counts and was thus the

185 count recorded. The level of precision between the final counts and those obtained independently
on a single occasion by another experienced reader of otoliths (S. A. Hesp) for a subsample of
otoliths from 100 *N. valenciennesi*, which covered a wide size range, was assessed using the
coefficient of variation (*CV*) 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, \bar{X}_j is the mean age estimate of the *j*th fish, and *R* is the number
190 of time each fish is aged (Chang 1982; Campana 2001). The resultant *CV* of 4.1% demonstrates
that there was strong agreement between the counts of the two readers.

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
195 the spawning period) of 1 March assigned to the members of the populations on both coasts (see
Results). Von Bertalanffy growth curves were then fitted to the lengths at age of the females and
males of *N. valenciennesi* using the Newton-Raphson method and employing the non-linear
regression routine in SPSS Inc. (2001). In the von Bertalanffy growth equation, L_t is the total
length (mm) at age *t* (years), L_∞ is the asymptotic length (mm) predicted by the equation, *k* is the
200 growth coefficient (year⁻¹) and t_0 is the hypothetical age (years) at which fish would have zero
length.

A likelihood-ratio test (Cerrato 1990) was used to compare the growth curves of the
females and males of *N. valenciennesi* caught on the south coast with those of the corresponding
sexes on the lower west coast. The test statistic was determined as twice the difference between
205 the log-likelihoods obtained by fitting a common growth curve to the data for the individuals on
the two coasts and by fitting separate growth curves for the individuals on each coast. 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 $\chi_a^2(q)$, 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 $\lambda = (-n/2)\ln(ss/n)$, where n refers to the sample size and ss refers to the sum of the squared residuals between the observed and expected lengths at age. The same procedure was used to determine whether the growth curves of females and males were significantly different.

215 *Duration and prevalence of spawning*

On the basis of their macroscopic characteristics, the gonads of each of the 984 fish that could be sexed were allocated to one of seven maturity stages, i.e. I = virgin; II = immature & resting; III = developing; IV = maturing; V = prespawning; VI = spawning and VII = spent, adapted from the criteria given by Laevastu (1965). The females and males that possessed gonads at stages III-220 VII in each year were considered likely to mature (stages III-V) or to have matured (VI-VII) during that year, have thus been referred to as mature.

In each month of sampling, gonads from a subsample of each sex, and which encompassed all gonad stages recorded in that month, were placed in Bouin's fixative for either 24 or 48h, depending on their size. The gonads were then dehydrated in a series of increasing 225 concentrations of ethanol and their mid-regions embedded in paraffin wax and cut into 6- μ m transverse sections. The sections were stained with Mallory's trichrome and examined using a compound microscope to confirm that gonads had been macroscopically assigned to an appropriate stage of maturity.

Mean monthly gonad weights for females and males of *N. valenciennesi* from offshore 230 waters of each coast were standardised for length using ANCOVA, employing month and coast

as fixed factors, length as the covariate and gonad weight as the dependent variable. The females and males used for this analysis of fish on the south coast were those ≥ 600 and 650 mm, respectively, which corresponded to the length above which all length classes contained $\geq 50\%$ of mature fish during the spawning season. As all females and males of *N. valenciennesi* collected from offshore waters of the lower west coast during the spawning period were mature, the mean monthly standardised gonad weights of both sexes were determined using data for all individuals on that coast. The same data were used to determine the monthly prevalences of the different gonadal stages in fish on the two coasts.

Although the prevalence of mature females and males in offshore waters of the south coast increased with total length, the pattern of change did not follow a logistic trend and thus the length at which maturity was reached by 50% of the individuals of each sex was taken as the length above which all length classes of the corresponding sexes contained $\geq 50\%$ of mature fish during the spawning season. Furthermore, as all or the vast majority of individuals in each length class of both the females and males of *N. valenciennesi* in lower west coast offshore waters were mature during the spawning period, a logistic curve was not fitted to the maturity data for those fish.

Results

Environmental measurements

Mean monthly water temperatures in inshore waters at Albany and Esperance on the south coast, which, in most months, differed by $< 1.5^{\circ}\text{C}$, rose from their minima of $14.5\text{-}15.7^{\circ}\text{C}$ in July and August to $21\text{-}22^{\circ}\text{C}$ in January and then declined to between $15.5\text{-}16.5^{\circ}\text{C}$ in June (Fig. 1). Trends in mean monthly offshore water temperatures at the three main sampling locations for

N. valenciennesi were similar; waters were always warmest at Rottnest Island, coolest at
255 Esperance and intermediate at Albany (Fig. 1).

Validation of ageing using otoliths

Alternating opaque and translucent zones were clearly visible in sectioned otoliths of
N. valenciennesi which contained at least one opaque zone (Fig. 2). The central region of the
260 otolith surrounding the primordium is opaque and large and the first opaque zone is relatively
wide and diffuse. Each opaque zone, which was most clearly defined on the ventral region of the
sectioned otolith, tends to become successively narrower towards the otolith periphery.

The mean monthly marginal increments for groups of otoliths with 2-4, 5-7 and 8-10
opaque zones were plotted for the two years which yielded the majority of fish. Although there
265 were no data for some months in both years, the trends exhibited by the mean monthly marginal
increments for those otolith groups in both years could still be seen to be similar. The marginal
increment data for corresponding calendar months in all years were thus pooled and provided
data for each group of otoliths in each calendar month. The mean monthly marginal increments
for otoliths with 2-4 opaque zones remained > 0.37 between September and November and then
270 declined precipitously a minimum in January, after which they increased progressively to June
(Fig. 3). The mean monthly marginal increments for otoliths with 5-7, 8-10 and > 10 opaque
zones followed essentially the same trend as that just described for otoliths with 2-4 opaque
zones, with values declining markedly to their minima in mid to late summer. Although the
number of fish with otoliths containing one opaque zone in many months was low, the trends
275 exhibited by the mean monthly marginal increments followed the same seasonal pattern as for
otoliths with a greater number of opaque zones (Fig. 3).

The autocorrelation coefficients, r , for the mean monthly marginal increments were only significant for lags of 1 month ($r = +0.44$; $p = 0.014$) and 5 months ($r = -0.51$; $p = 0.004$), but were almost significant for a lag of 11 months ($r = +0.36$; $p = 0.060$). Thus, the mean monthly marginal increments show a periodicity, becoming out of phase at approximately half a year and coming back into phase at a lag of approximately 1 year. These results are consistent with the formation of a single opaque zone each year. The single pronounced decline and then progressive increase undergone during the year by the mean monthly marginal increments for otoliths with different numbers of opaque zones demonstrate that, irrespective of the number of opaque zones, a single opaque zone is typically formed annually in the otoliths of *N. valenciennesi*. The number of opaque zones in those otoliths can thus be used to age the individuals of this species.

The smallest *N. valenciennesi* measured 157 mm TL (= 133 mm FL) and was caught in February (late summer) and the next two smallest individuals, measuring 185 mm TL (= 157 mm FL) and 197 mm TL (= 167 mm FL), were caught in May (late autumn) and June (early winter), respectively. Because of the paucity of *N. valenciennesi* at lengths < 200 mm TL, i.e. = 170 mm FL (Fig. 4), it is helpful to consider the early and similar pattern of growth of the cheilodactylids *N. macropterus* and *C. spectabilis*, for both of which there were more extensive data (Jordan 2001a; Ewing *et al.* 2007). Those studies showed that, by 1 year of age, *N. macropterus* and *C. spectabilis* had attained fork lengths of 145 and 132 mm, respectively. As these fork lengths are similar to that of the smallest *N. valenciennesi* caught just before the birth date of 1 March for this species, and slightly less than those of the next two smallest *N. valenciennesi* and which were caught 3-4 months later, it is highly likely that the first individual was approaching 1 year old and the other two were 3-4 months older.

300 The otoliths of the smallest *N. valenciennesi* were too damaged during capture to be used.
The otoliths of the two small individuals (185 and 197 mm TL) caught in late autumn and early
winter contained a large, central opaque region and a surrounding translucent area (Fig. 2a). In
contrast, the otoliths of individuals measuring 294, 297 and 299 mm TL in December contained
a single, recently-formed and diffuse opaque zone that had become delineated from the otolith
305 edge through the presence of a narrow translucent zone at the otolith margin (Fig. 2b). The
preceding confamilial comparisons and descriptions of the otoliths of small *N. valenciennesi*
provide strong circumstantial evidence that, as in *C. spectabilis* (Ewing *et al.* 2007), the first
opaque zone is not laid down until the second winter of life, at which time *N. valenciennesi* is on
average ~ 16 months old. It would thus follow that those *N. valenciennesi* caught with one
310 newly-formed opaque zone in December were approximately 22 months old. An increase in
length from nearly 200 mm TL or 170 mm FL in June to nearly 300 mm TL or 256mm FL in
December is consistent with the rapid growth exhibited by cheilodactylids early in life (see Fig. 9
in Discussion) and that this period included the spring and early summer when the growth of
fishes is typically fast.

315

Length and age compositions and growth

The *N. valenciennesi* collected by spear fishing (inshore), recreational line fishing (offshore) and
commercial gill netting (offshore) ranged in total length from 157 to 868 mm (\bar{x} = 494 mm), 404
to 984 mm (\bar{x} = 653 mm) and 442 to 958 mm (\bar{x} = 682 mm), respectively, and in age class from
320 0+ to 16+, 3+ to 19+ and 3+ to 21+ years, respectively (Fig. 4). The 985 *N. valenciennesi*, whose
gonads had not been removed and which could thus be sexed, ranged in length and age class

from 157 to 846 mm and 1+ to 19+ years for females and from 192 to 984 mm and 1+ to 19+ years for males.

Although the growth curves of the females and males on the south coast differed significantly from those of the corresponding sexes on the lower west coast ($P < 0.05$), the difference in the lengths of the corresponding sexes, estimated from those curves, was always < 4% at each age between 5 and 12 years, the ages that were best represented in the samples (Fig. 5). These regional differences in the growth of each sex on the two coasts were considered of limited biological significance and consequently the lengths at age of females and of males in the two regions were combined to produce a single growth curve for each sex across both regions (Fig. 5). The resultant growth curves for the females and males of *N. valenciennesi* were significantly different ($P < 0.001$).

The von Bertalanffy growth curves provided a good fit to the lengths at age of the individuals of females and males (Fig. 5; Table 1). On average, at ages of 5, 7, 10, 13 and 15 years, the females attained lengths of 550, 615, 662, 682 and 688 mm, compared with 583, 673, 752, 793 and 809 mm by the males.

Duration and prevalence of spawning

As the majority of *N. valenciennesi* caught in inshore waters on the south coast were immature, the mean monthly standardised gonads weights were not calculated for fish in these waters. The mean monthly standardised gonad weights for female *N. valenciennesi* > 600 mm (*i.e.* approximate average size at first maturity on this coast) in offshore south coast waters rose from low levels in July to October to a maximum in March, before declining progressively to a low

level in June (Fig. 6a). The mean monthly standardised gonad weights of male *N. valenciennesi*
345 in offshore south coast waters peaked one month earlier and at a far lower level (Fig. 6b).

As all or the majority of each length class of both the females and males of
N. valenciennesi in offshore waters of the lower west coast were mature during the spawning
period (Fig. 7e, f), the mean monthly gonad weights for fish in these waters were calculated
using the gonadal data for all fishes caught in those waters. Although the mean monthly gonad
350 weights for female and male *N. valenciennesi* in offshore waters of the lower west coast
displayed a similar seasonal trend to those of females and males in offshore waters of the south
coast, their maxima were far greater, i.e. 126 vs 52 g and 54 g vs 20 g, respectively (Figs 6a-d).

Females and males with gonads at stages between III and VII were caught in offshore
south coast waters only between December and June and between January and April,
355 respectively, with peaks in March and February, respectively (Figs 6a, b). All but one of the
females taken in offshore waters of the lower west coast between November and May contained
ovaries at one of stages III to VII (Fig. 6c) and males with the corresponding gonadal stages were
caught in those waters between December and May (Fig. 6d). All females and males obtained
from outside the above respective periods possessed gonads at stages I or II.

360 The trends exhibited by the mean monthly female and male gonad weights and whether
or not females and males with gonads at stages V or VI were present indicate that
N. valenciennesi spawn between November (late spring) and June (early winter) in south-western
Australia. As 1 March represented the approximate mid-point of the spawning period, it was
chosen as the birth date for *N. valenciennesi*.

365 *Lengths and ages at maturity*

Few mature females or males of *N. valenciennesi* were caught in inshore waters of the south coast during the spawning period of this species (Fig. 7a, b), whereas the percentage of mature females in offshore waters of the south coast increased from 12% in fish of 500 to 549 mm to ~ 50% in those of 600 to 699 mm and 100% in those > 750 mm (Fig. 7c). Similar trends occurred with males (Figs 7b, d). Although the prevalence of mature females and males in offshore waters of the south coast increased with total length, the pattern of change did not follow a logistic trend (Figs 7c, d). The approximate lengths at which maturity was attained by 50% of females and males were 600 and 650 mm, respectively. Although the total length ranges of females and males in offshore waters of the lower west coast were similar to those on the south coast, the majority of females (89%) and males (82%) caught on the lower west coast during the spawning season were mature, whereas this applied to only 48 and 43%, respectively, of those on the south coast (c.f. Figs 7c-f).

None of the females that were caught in inshore waters of the south coast and were < 5 years old were mature and the same was true of males < 10 years old (Figs 8a, b). In south coast offshore waters, the percentage frequency of occurrence of mature females was < 35% in each age class between 4 and 7 years, but subsequently increased to 100% in fish \geq 13 years (Figs 8c-d). In contrast, the majority of female and male *N. valenciennesi* caught in offshore waters of the lower west coast, which ranged from 3-17 years old, were mature (Figs 8e-f).

385 **Discussion**

Ageing and growth

The necessity to section particularly the larger otoliths of *N. valenciennesi* to reveal all of their opaque zones appears to parallel the situation with *N. macropterus*. In the latter species, the

number of opaque zones recorded in sectioned otoliths of fish from Tasmania were far greater
390 than those reported previously employing whole otoliths of similar-sized individuals of that
species in New South Wales (cf. Smith 1982; Jordan 2001a; Table 2). Our use of marginal
increment analysis for sectioned otoliths of *N. valenciennesi* demonstrated that, irrespective of
the number of opaque zones in an otolith, a new opaque zone was typically formed annually in
each otolith. It was therefore valid to use the number of opaque zones visible in sectioned
395 otoliths of *N. valenciennesi* for ageing this cheilodactylid, but this approach needed to take into
account that such a zone is not laid down during the first winter of life and consequently just
after the main period of spawning. As with *N. macropterus* in Tasmania (Jordan 2001a) and
N. valenciennesi in our study, the number of opaque zones in sectioned otoliths was employed to
age *C. fuscus* in New South Wales (Lowry 2003) and *C. spectabilis* in Tasmania (Murphy and
400 Lyle 1999). In the latter species, validation that the opaque zones in their otoliths are formed
annually included the use of oxytetracycline and bomb radiocarbon methods (Ewing *et al.* 2007).

Nemadactylus valenciennesi, *N. macropterus*, *C. fuscus* and *C. spectabilis* each grew at
a similar rapid rate during the first three years of life and, after a similar age, all species exhibited
little further increase in length (Fig. 9). Thus, 90% of the estimated asymptotic lengths of the
405 four species had been attained by 5-8 years by their females and 6-11 years by their males. The
ages at which this occurred relative to the longevity of a species varied markedly, however,
among the four cheilodactylid species. For example, among females, that age represented as little
as 10% of the maximum recorded age for *C. spectabilis*, compared with 23% for
N. macropterus, 27% for *C. fuscus* and as much as 42% for *N. valenciennesi*. These comparisons
410 highlight the fact that, in comparison with *N. valenciennesi*, some *C. spectabilis*, as pointed out
by Ewing *et al.* (2007), spend a remarkably long period undergoing little increase in length. The

same is true, but to a lesser extent, for *N. macropterus* and *C. fuscus*. Growth became so restricted in *C. spectabilis* that, if an individual had lived to the maximum age of 97 years, its length would have increased by only about 10% in the last 90 years (Fig. 9).

415

Movements, sexual maturation and spawning

All *N. valenciennesi* < 400 mm TL were caught by spear fishing the low granite reefs of island and inshore shallow waters (<20m depth) along the southern coast of W.A. Although *N. valenciennesi* occupies a similar rugose boulder habitat to that of *C. fuscus* in eastern Australia (Lowry and Suthers 1998), it does not exhibit the same tendency to shelter in reef crevices during the day. Because *N. valenciennesi* could be readily sighted and speared in their nearshore reef habitat, the samples obtained by spear fishing are considered broadly representative of this species in those waters. As few of even the larger *N. valenciennesi*, i.e. > 400 mm TL, caught in these waters were mature, these waters not only act as a nursery area but provide a habitat for large immature fish. Our failure to catch or even observe the juveniles of *N. valenciennesi* in comparable inshore waters along the lower west coast is consistent with the absence or rarity of this species in extensive underwater surveys of sites in those nearshore waters (e.g. Hutchins and Thompson 1983; Hutchins 2001).

Although the length ranges of both females and males of *N. valenciennesi* caught over granite reefs in offshore south coast waters were similar to those of the corresponding sexes collected using the same methods over limestone reefs in offshore lower west coast waters, the prevalence of mature fish in the two regions differed markedly. Thus, whereas mature fish broadly increased in prevalence from low levels in the smaller individuals to 100% in the larger

individuals caught in offshore south coast waters, the majority or all fish in each length class in
435 offshore lower west coast waters were mature.

From the above comparisons, it is proposed that juvenile *N. valenciennesi* are largely confined to the south coast and that, as they increase in size, substantial numbers move to the lower west coast where they soon become fully mature and spawn. In contrast, the other large individuals of this species in inshore south coast waters move outwards into offshore waters on
440 that same coast, where they take longer to mature. This is corroborated by charter boat operators who often catch small *N. valenciennesi* in nearshore waters, but fishing in offshore waters using the same gear catch fish always exceeding the minimum legal length of 410 mm (T. Little, pes. comm). A size-related movement from reefs in inshore to those in offshore waters on the south coast parallels the movement patterns of the co-occurring western blue groper, *Achoerodus*
445 *gouldii*, which likewise makes a major contribution to the demersal gill net fishery on that coast (Coulson *et al.* 2009). It also parallels that exhibited by *N. macropterus* in Tasmania (Jordan 2001b) and *C. spectabilis* in New Zealand (Leum and Choat 1980; McCormick 1989a). The suggestion that many *N. valenciennesi* move from the south to lower west coast for spawning parallels, to a large extent, the movement patterns proposed by Smith *et al.* (2004) for the
450 champagne crab *Hypothalassia acerba* and by Wakefield (2008) for the snapper *Pagarus aratus*. This suggests that, for certain species, conditions on the lower west coast are more favourable for gonadal development and maturation, possibly through, for example, the presence of higher water temperatures (Fig. 1) and/or differences in the quality and/or quantity of food.

Despite the presence of substantial numbers of fully-mature *N. valenciennesi* on the
455 lower west coast, sampling for fish larvae in waters near those where mature fish were caught yielded only five cheilodactylid larvae (Muhling 2006). In contrast, *Nemadactylus* larvae were

abundant in plankton samples collected by Fletcher *et al.* (1996) in offshore waters of the south coast in the winter, i.e. following the spawning period of *N. valenciennesi*. These results suggest that, after *N. valenciennesi* spawns on the lower west coast, their larvae are rapidly transported southwards and then become distributed eastwards along the south coast. Such a proposed movement by larvae would coincide with the time when the Leeuwin Current, which flows southwards and eastwards, is at its strongest (Smith *et al.* 1991). Transport over such a substantial distance would be facilitated not only by that strong current, but also by the length of the pelagic larval phase of cheilodactylids, which lasts for several months (Vooren 1972; Bruce *et al.* 2001). The ability of cheilodactylid larvae to be transported over long distances by the movements of large water masses has been demonstrated to occur in *N. macropterus* in Tasmania (Bruce *et al.* 2001).

Comparisons between the life cycle characteristics of cheilodactylid species

Certain life cycle characteristics of the four species of the Cheilodactylidae examined diverge markedly (Table 2). In terms of longevity, *C. spectabilis* lies at one end of the spectrum, with maximum recorded ages of 94 years for females and 97 years for males (Ewing *et al.* 2007), while *N. valenciennesi* occupies the other end, with a maximum age of 19 years for both sexes and 21 years for an unsexed individual. Despite their far greater longevity, the maximum recorded fork lengths for females (496 mm) and males (552 mm) of *C. spectabilis* (Murphy and Lyle 1999) were far less than for those sexes of *N. valenciennesi* (731 and 853 mm, respectively), the latter of which corresponds to a total length similar to the maximum recorded for *N. valenciennesi* throughout its range (Gomon *et al.* 2008). Yet, the females of *C. spectabilis* (Murphy and Lyle 1999) and *N. valenciennesi* both typically mature at a young age (~ 5 years).

480 The maximum fork lengths recorded for the females and males of *N. macropterus* by
Jordan (2001a) and for *C. fuscus* by Lowry (2003) are similar to those of *C. spectabilis* and thus
far lower than those of *N. valenciennesi*. However, the maximum recorded ages of 41 and 40
years, respectively, for the first two species are far less than those of *C. spectabilis*, but
substantially greater than those of *N. valenciennesi* (Table 2). Yet, as with the other
485 cheilodactylid species, *N. macropterus* matures at a young age, i.e. ~3 years (Jordan 1998). Thus,
the age at maturity is not related to longevity in the Cheilodactylidae, or even among its
congeners, i.e. *Nemadactylus* spp. and *Cheilodactylus* spp. This contrasts with the situation
typically found with a range of taxa, including fishes, in which the age at maturity is positively
correlated with longevity (e.g. Beverton 1963; Charnov and Berrigan 1990; Froese and Binohlan
490 2000; Charnov *et al.* 2001; Mangel and Abrahams 2001).

Froese and Binohlan (2000) used data for numerous fish species to produce several
equations, one of which related lengths at maturity to asymptotic lengths, while another related
maximum ages to ages at maturity and another related asymptotic lengths to maximum lengths.
The asymptotic lengths (derived from the third equation in the case of *C. spectabilis*) and ages
495 for female *N. valenciennesi*, *N. macropterus* and *C. spectabilis* at maturity were inserted into the
respective equations to calculate, for the females of each of those species, the ranges in their
predicted lengths at maturity and predicted maximum ages (as determined by back calculations
from the range of two standard errors on either side of the predicted value of the log of the
respective variable). Note that there are no reproductive data for *C. fuscus*. The lengths at which
500 female *N. valenciennesi*, *N. macropterus* and *C. spectabilis* mature lie within the ranges of the
lengths at maturity predicted for each of those species by the first equation. Likewise, the
maximum recorded age for female *N. valenciennesi* lies within the range of ~ 7 to 40 years

predicted by the second equation for the maximum age of its females on the basis of their age at maturity. In contrast, the maximum age estimated for female *N. macropterus*, and even more markedly for female *C. spectabilis* (see also Ewing *et al.* 2007), lie well beyond the ranges of maximum ages predicted by the second equation for the females of those species (*i.e.* ~ 4 to 25 years and 7 to 40 years, respectively) after the respective ages at maturity had been inserted into that equation. Thus, for female *N. valenciennesi*, the relationships between length at maturity and asymptotic length and between age at maturity and maximum life span are both consistent with those typically exhibited by other fish species. In contrast, although the asymptotic lengths of female *N. macropterus* and *C. spectabilis* are consistent with those predicted from their lengths at maturity, their maximum ages are far greater than those predicted from their ages at maturity.

While the maximum life spans of *N. macropterus* and *C. spectabilis* are not consistent with those predicted from their ages at maturity, this is not the case with *Sebastes* species (rockfishes), whose life spans cover the remarkable range of 12 to ~ 205 years (Mangel *et al.* 2007). Furthermore, and also unlike *N. macropterus*, *C. fuscus* and *C. spectabilis*, the growth of long-lived *Sebastes* species does not typically level off abruptly after the very early years in life (e.g. Butler *et al.* 2003; Saborido-Rey *et al.* 2004; Stransky *et al.* 2005).

A particular combination of the growth characteristics and age at maturity of a species is assumed to maximise lifetime reproductive output (*i.e.* reproductive fitness) in response to the level of natural mortality to which that species has been subjected (Charnov *et al.* 2001; Lester *et al.* 2004). The unexpectedly early ages of *N. macropterus* and *C. spectabilis* at maturity and the confinement of their growth largely to the very early years of their long lives suggest that the development of initial rapid growth and an early attainment of maturity in these species could have resulted from selection pressures arising from a far higher mortality of smaller and younger

fish. Conversely, there would be no obvious advantage for maturity to be delayed in *N. macropterus* and *C. spectabilis* because the growth curves of these species exhibit a marked tendency to level off very early in life (Fig. 9, Jordan 2001a; Ewing *et al.* 2007) and thus any such delay would not result in a sufficient increase in reproductive output throughout the remainder of life to offset mortality.

The question now remains as to why *N. macropterus* and *C. fuscus* and particularly *C. spectabilis* should have much longer life spans than *N. valenciennesi*, which belongs to the same small family. In broad terms, an extended life span can evolve only when mortality rates are sufficiently low to allow individuals to live to an old age without a high probability of death from accidental causes (Mangel and Abrahams 2001). Long life spans have often been considered to have evolved in response to variable or episodic recruitment in fluctuating environments (e.g. Murphy 1967; Longhurst 2002; Mangel *et al.* 2007). Although the age-frequency and/or length at age data for *N. macropterus*, *C. fuscus* and *C. spectabilis* (Jordan 2001a; Lowry 2003; Ewing *et al.* 2007) provide little evidence that the annual recruitment of these species varies greatly, such a situation may have occurred in the past. The constraint of growth throughout much of the extended life spans of the above three species suggests that their growth has been or is limited in some way by environmental factors, such as the availability of food and/or space. Since their body size increases little throughout adult life, annual fecundity will not exhibit the same marked increase with age as typically occurs with other fish species. The extended life spans of *N. macropterus*, *C. fuscus* and *C. spectabilis* could thus represent the results of selection pressures, which ensure that these species have the opportunity to spawn over many years and are therefore able to exhibit sufficient lifetime reproductive output to sustain the population. On the basis of other studies, it is likely that the longer life spans of *N. macropterus*,

C. fuscus and *C. spectabilis* than *N. valenciennesi* are accompanied by a greater investment of
550 energy in maintaining the cells, tissues and organs of those species and thus preventing the
accumulation of cellular damage (e.g. Holliday 1997; Kirkwood *et al.* 2003; Mangel *et al.* 2007).

In summary, the life cycle traits of *N. valenciennesi* are typical of those exhibited by the
majority of fish species and thus highlight the extent to which those of *N. macropterus* and
particularly *C. spectabilis* diverge from the normal pattern. While species in the genus *Sebastes*
555 range even more widely than those of the above cheilodactylid species in terms of their life
spans, they reach maturity at an age that is consistent with their maximum age (Mangel *et al.*
2007). Comparisons between the life cycle characteristics of closely and distantly-related taxa
led us to hypothesise that, under certain circumstances, far greater mortality of the smaller and
younger individuals of a species and/or constraints on the growth of its adults may play major
560 roles in selecting for early maturity and a long life.

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Figure 1. Mean monthly water temperatures ± 1 SE for a) inshore waters at Albany (grey circles) and Esperance (black circles) on the south coast of Western Australia and b) offshore waters at Albany (grey circles) and Esperance (black circles) and at Rottnest (black triangles) on the lower west coast of Western Australia. On the x-axis, closed rectangles refer to winter and summer months and the open rectangles to spring and autumn months.

Figure 2. Sectioned otoliths of *Nemadactylus valenciennesi* with a) 0, b) 1, c) 3, d) 8 and e) 17 opaque zones, showing the large central opaque region surrounding the primordium and with the opaque zones in b-e being denoted by white points (\circ). Scale bars = 0.5 mm.

Figure 3. Mean monthly marginal increments ± 1 SE on sectioned sagittal otoliths of *Nemadactylus valenciennesi* with different numbers of opaque zones. Sample sizes are given above each mean. On the x-axis, closed rectangles refer to winter and summer months and the open rectangles to spring and autumn months.

Figure 4. Length and age-frequency distributions for *Nemadactylus valenciennesi* caught by spear fishing (grey histograms) in inshore waters and recreational line fishing (black histograms) and commercial gillnetting (white histograms) in offshore waters. n_s , n_r , and n_g ; number of fish caught by spear fishing, recreational line fishing and gill netting, respectively.

Figure 5. von Bertalanffy growth curves fitted to the lengths at age of females and males of *Nemadactylus valenciennesi*. n = sample size.

Figure 6. Mean monthly gonad weights ± 1 SE and monthly percentage frequencies of occurrence of sequential stages in the gonadal development of *Nemadactylus valenciennesi*. a) Females ≥ 600 mm and b) males ≥ 650 mm from south coast offshore waters and c) all females and d) all males from lower west coast offshore waters. The cut-off lengths for females and

750 males on the south coast are those at which approximately 50% of those two sexes become
mature, while all females and males were included for the west coast as virtually all individuals
became mature during the spawning season on that coast. Gonad weights were calculated for a
standard length of 654 mm for females and 732 mm for males. Histograms for stages III & IV, V
& VI and VII are shown in light grey, dark grey and white, respectively. On the x-axis, closed
755 rectangles refer to winter and summer months and the open rectangles to spring and autumn
months. Sample sizes are given above each mean.

Figure 7. Percentage frequency of occurrence of the females and males of *Nemadactylus
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the spawning period from a) and b) south coast inshore waters, c) and d) south coast offshore
760 waters and e) and f) lower west coast offshore waters. Sample sizes are given above each
histogram.

Figure 8. Percentage frequency of occurrence of the females and males of *Nemadactylus
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spawning period from a) and b) south coast inshore waters, c) and d) south coast offshore waters
765 and e) and f) lower west coast offshore waters. Sample sizes are shown above each histogram.

Figure 9. Growth curves for females and males of *Nemadactylus valenciennesi*, *Cheilodactylus
spectabilis*, *Nemadactylus macropterus* and *Cheilodactylus fuscus*. von Bertalanffy growth
curves were used for each species except for *C. spectabilis* for which the Schnute growth curve
was employed. Data for *N. macropterus*, *C. fuscus* and *C. spectabilis* were obtained from Jordan
770 (2001a), Lowry (2003) and Ewing *et al.* (2007), respectively.

Table 1. The von Bertalanffy growth parameters L_{∞} , k and, t_0 , and their upper and lower 95% confidence limits, for females and males of *Nemadactylus valenciennesi* in south-western

775 Australian waters. L_{∞} is the asymptotic total length (mm), k is the growth coefficient (year^{-1}), t_0 is the hypothetical age (years) at which fish would have zero length, r^2 is the coefficient of determination and n is the number of fish.

		L_{∞}	k	t_0	r^2	n
Female	Estimate	696	0.29	-0.36	0.86	356
	Upper	713	0.33	-0.07		
	Lower	678	0.25	-0.65		
Male	Estimate	839	0.22	-0.52	0.80	460
	Upper	870	0.25	-0.17		
	Lower	808	0.18	-0.87		

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Table 2. Maximum fork length (FL_{max} in mm), maximum age (A_{max} in years), and typical lengths and ages at first maturity (L_{mat} in mm FL, A_{mat} in years) of *Nemadactylus valenciennesi* and other species of the Cheilodactylidae for which there are substantial data. While von Bertalanffy growth parameters are provided for *N. valenciennesi*, *Nemadactylus macropterus* and *Cheilodactylus fuscus*, Ewing *et al.* (2007) used the Schnute growth curve for *C. spectabilis* because it provided a better fit than the von Bertalanffy growth curve. L_{∞} is the asymptotic fork length (mm), k is the growth coefficient ($year^{-1}$), t_0 is the hypothetical age (years) at which fish would have zero length, s refers to south coast and w to lower west coast in south-western Australia. Data for *N. macropterus* and *C. fuscus* were taken from Jordan (1998; 2001a) and Lowry (2003), respectively, while those for *C. spectabilis* were from Murphy and Lyle (1999) and Ewing *et al.* (2007).

	Sex	FL_{max}	A_{max}	L_{∞}	k	t_0	L_{mat}	A_{mat}
<i>Nemadactylus valenciennesi</i>	Female	731	19	599	0.29	-0.36	600(s) 400(w)	8(s) 3(w)
	Male	853	19	725	0.22	-0.52	650(s) 500(w)	7(s) 3(w)
<i>Nemadactylus macropterus</i>	Female	455	30	384	0.33	0.40	250	3
	Male	423	41	362	0.42	0.15	270	3
<i>Cheilodactylus fuscus</i>	Female	460	34	376	0.22	-3.60		
	Male	450	40	454	0.13	-5.39		
<i>Cheilodactylus spectabilis</i>	Female	496	94				324	4-5
	Male	552	97					

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