

Validation of age and growth in a long-lived temperate reef fish using otolith structure, oxytetracycline and bomb radiocarbon methods

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Abstract. Generating age estimates for long-lived fish requires particular attention to validation because they are usually difficult to age owing to narrow increment structure. A robust validation of the accuracy and precision of banded morwong, *Cheilodactylus spectabilis*, sampled from Tasmanian waters, was undertaken. Age at the first enumerated increment was established from analysis of juvenile cohorts, and the timing and periodicity of increment formation was established using a quantitative model from oxytetracycline (OTC) mark-recaptures at liberty for periods of up to 8 years. The accuracy of age estimates was examined independently by comparing radiocarbon values in the otolith region corresponding to the first year of growth against the south-western Pacific calibration curve. *C. spectabilis* is very long-lived, with males and females living to over 90 years of age. Growth modelling revealed a fast initial growth phase, terminating in an abrupt plateau near the asymptotic length. This species displays substantial sexual dimorphism in growth, with males growing to larger sizes than females.

Additional keywords: cheilodactylidae, longevity.

Introduction

The interpretation of periodic increment structure in fish bony parts is a fundamental tool in estimating age structure, growth and mortality of fish populations. Otoliths are often used for this purpose because they incorporate incremental structure on a daily, seasonal and/or annual basis. Within age and growth research, however, there has been a history of inadequate attention to validation (Beamish and McFarlane 1983; Kalish 1993), with recent consideration given to the neglected distinction between validation of the periodicity of increment formation and that of the accuracy of age estimates (Campana 2001). Other factors, such as sub-annual macrostructure before the first annual zone (Kerstan 1995; Mann Lang and Buxton 1996; Karlou-Riga 2000) emphasise the necessity to determine the position of the first annulus (Francis *et al.* 1992; Campana 2001). An understanding of the timing of increment formation is also necessary to interpret the otolith growing edge (Fowler and Short 1998; Cappel *et al.* 2000; Williams *et al.* 2005).

The otoliths from temperate fish species have been reported to display clear increment structure (Morison *et al.* 1998; Ewing *et al.* 2003; Tracey and Lyle 2005) promoting their use for age

estimation. However, temperate waters have also yielded several particularly long-lived species that, because of narrow increment structure and large numbers of age classes, present challenges to age estimation and validation. Transverse sectioning of otoliths generally improves the detection of increment structure, particularly in long-lived fish where age estimates derived from unsectioned otoliths can underestimate age (Beamish 1979; Campana 1984; Hyndes *et al.* 1992). Mark-recapture methods, such as oxytetracycline (OTC) otolith marking are valuable for such long-lived species, particularly if long times at liberty are achieved, because they validate otolith growth over the entire period at liberty.

Methods that measure absolute age, such as bomb radiocarbon analyses, allow the accuracy of age estimates to be calculated (Kalish 1993). The bomb radiocarbon chronometer, considered one of the best age validation approaches available for long-lived fish (Campana 2001), uses the temporally discrete pulse of radiocarbon that was formed in the atmosphere as a result of extensive atmospheric testing of nuclear weapons in the 1950s and 60s (Kalish 1995b). Through gas transfer, a portion of atmospheric oxidised radiocarbon ($^{14}\text{CO}_2$) becomes incorporated

in the ocean as dissolved inorganic carbon (DIC). As otoliths incorporate DIC from the water column, and this material is not resorbed during the life of the fish, absorbed radiocarbon leaves a detectable record in fish otoliths (Kalish 1993, 1995b; Campana 1999). The greatest accuracy of the bomb radiocarbon chronometer is for fish born in the period from 1960 to 1974, when the rate of increase of radiocarbon in the ocean was greatest, and for fish that inhabit well-mixed surface waters of the ocean, because deepwater mixing rates are slow and variable (Kalish 2001). The bomb radiocarbon chronometer has been used recently to validate ageing methodologies for several species (Kalish *et al.* 1996; Campana 1997; Kerr *et al.* 2004; Piner and Wischniowski 2004; Andrews *et al.* 2005). An age calibration curve based on otolith radiocarbon in the otoliths of *Pagrus auratus* has been produced for the surface waters of the south-western Pacific (Kalish 1993), enabling validation of age estimates for other species from the region by comparing their radiocarbon concentrations with the calibration curve.

Banded morwong, *Cheilodactylus spectabilis*, is a large temperate fish that is common on shallow reefs of south-eastern Australia and north-eastern New Zealand (Leum and Choat 1980; Gomon *et al.* 1994). Spawning occurs in late summer to early autumn (mainly between March and April), and females appear to be serial spawners (McCormick 1989a). Consistent with other Cheilodactylids, such as *Nemadactylus macropterus* (Vooren 1972; Bruce *et al.* 2001; Jordan 2001), *C. spectabilis* has a prolonged pelagic larval stage of around 180 days (Wolf 1998), with larvae encountered in surface waters up to 200 km off the coast of Tasmania (Bruce *et al.* 2001). Before settlement on shallow inshore reefs, *C. spectabilis* metamorphose into a post-larval 'paper-fish' that is characterised by a very thin laterally compressed body with a sharply keeled belly. Once settled, individuals appear to remain more or less site attached, with tagging studies indicating very limited movement (Murphy and Lyle 1999).

Cheilodactylus spectabilis is a key species in the live fish trade in Australia, and is targeted with gill-nets in Tasmania and Victoria (Murphy and Lyle 1999). Preliminary studies indicated that *C. spectabilis* may be a long-lived species (Murphy and Lyle 1999). This, along with life history characteristics such as site-attachment may increase vulnerability to over-exploitation and necessitate the development of a validated ageing protocol to allow issues of growth, age structure, and recruitment variability to be assessed. The aim of the present study was to establish a robust ageing methodology for *C. spectabilis* which included: ageing of otolith inner structures, estimation of the periodicity, timing and rate of formation of otolith increment structure, and measurement of the precision and accuracy of subsequent age estimates. Age estimates and size data were used to model growth to assess the extent of sexual dimorphism observed during sampling.

Materials and methods

Sampling

Cheilodactylus spectabilis were sampled over the period 1995 to 2005, from inshore coastal rocky reefs on the east coast of Tasmania, generally in less than 25 m of water. Otoliths from around 3400 individuals were available for age estimation. Over

97% of these fish were sampled in spawning season closures (March–April) of 1996, 1997, and annually between 2001 and 2005. Standard commercial fishing gear (gill-nets of mesh size 133–140 mm) were used to collect samples. As these gill-nets generally selected fish larger than 250 mm fork length (FL), sampling for smaller individuals was undertaken by hand-net (after underwater application of quinaldine) and by hand-spear in inshore subtidal rock pools and shallow sheltered rocky reefs. Small fish up to 150 mm FL were predominantly caught in 1995 and 1996 by hand net (Wolf 1998), whereas fish between 130 and 280 mm FL were sampled opportunistically by hand spear between 2001 and 2005.

During 1995 and 1996, 1375 *C. spectabilis* were injected with OTC (Engemycin 100) at a rate of 50 mg kg⁻¹ (McFarlane and Beamish 1987), marked with T-bar tags and released. Of the recaptured fish, otoliths were available from 94 fish that had been at liberty for periods ranging from 43 to 3102 days.

Laboratory procedures

Each fish was sexed and fork length to the nearest mm was recorded. Sagittal otoliths (hereafter 'otoliths') were removed, cleaned, dried, and if intact, weighed to the nearest mg. Otoliths from OTC tag-recaptures were stored in lightproof containers to minimise degradation of fluorescent marks.

Otolith preparation and interpretation

The terminology used in this paper is based on Kalish *et al.* (1995). One otolith from each fish was mounted in a block of polyester casting resin and sectioned with a diamond lapidary saw transversely through the primordium to a thickness of 250–300 µm. Sections were mounted on a glass slide with polyester resin. Each mounted section was examined with a stereo-microscope at 25× magnification using transmitted light to count opaque zones and to categorise the otolith marginal increment as wide, medium or narrow relative to the width of the next inner translucent zone. Otoliths were rejected if the increment structure was optically unclear or if the primordium could not be identified. Otoliths were examined with no reference to fish length or date sampled.

Interpretation of inner structure

Fish from the juvenile dataset were grouped into 'cohorts' on the basis of fish length, otolith size and otolith structure. Analysis of the visual characteristics and dimensions of the otoliths from these juveniles were also used to assign 'ages' to equivalent components of the inner structure of otoliths from the sample of larger fish.

Periodicity and timing of opaque zone formation

Otolith sections from recaptured banded morwong were viewed under blue-ultraviolet light to detect the presence and position of a fluorescent mark from OTC injection at the time of original capture. The periodicity and timing of formation of opaque zones was estimated directly from OTC recaptures using the model proposed by Cappo *et al.* (2000). The model generates a 'liberty fraction' (LF):

$$LF = IF + N + FF \quad (1)$$

where *N* is the number of completed increment cycles beyond an OTC mark (increment cycles were considered to start at the

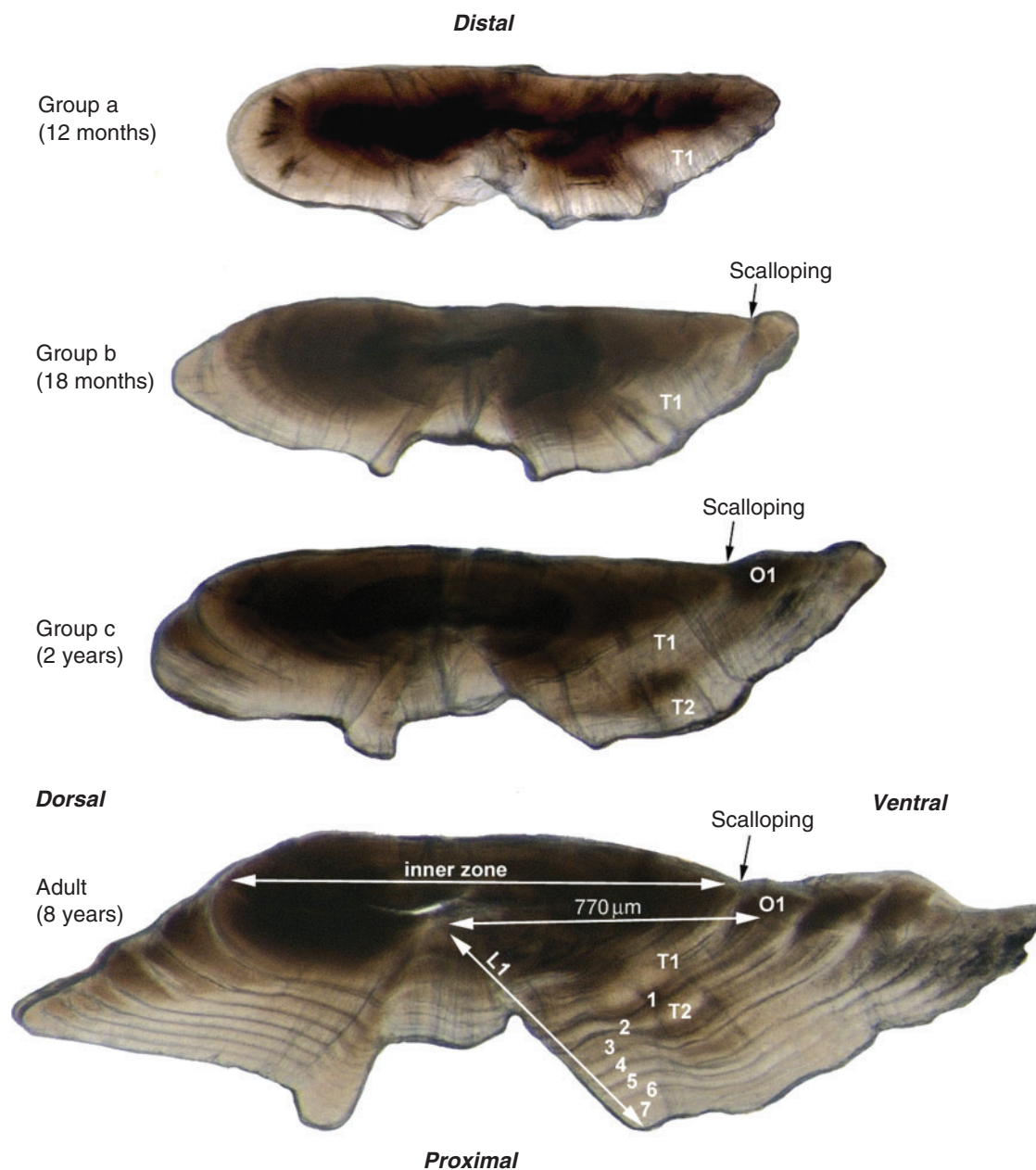


Fig. 1. Photomicrographs, taken using transmitted light, of representative transverse otolith sections from the *Cheilodactylus spectabilis* juvenile sample (groups a, b and c) and a representative section from the adult sample. T1 refers to the distinctive translucent zone used to assist in the detection of O1, which is the first enumerated zone. Otolith images are at the same scale, which is indicated by the mean distance from the primordium to O1 in the adult section. The axis along which radii for the oxytetracycline (OTC) model were measured is indicated by L1. Opaque zones are marked and numbered and the age calculated from this count was 8 years.

completion of an opaque zone); *IF*, the initial fraction, is the proportion of the increment cycle containing the OTC mark that is deposited beyond the mark; and *FF*, the final fraction, is the width of the material deposited at the otolith growing edge beyond the last complete increment cycle, expressed as a proportion of the last complete increment cycle. Partial increment cycles were calculated from otolith radii measured on the L1 Plane (Fig. 1) using image analysis software on digitised images taken with a compound microscope at 100× magnification. This

model assumes that the increment cycles near the otolith growing edge are of equal width. Measurements were made with no reference to the time of release and subsequent recapture. The increment cycle frequency was investigated using linear regression:

$$LF = aL + b \quad (2)$$

where *L* is the time at liberty in years, *a* is the slope and *b* is the intercept. The accuracy of counts of annual increments was

derived from the significance of any departure from an intercept of zero and from a unitary slope. Closing dates were estimated using the model according to Cappelletti *et al.* (2000) as:

$$CD = t - 365(FF/V) \quad (3)$$

where t is the date of capture and V is the cycle frequency determined as:

$$V = LF/L \quad (4)$$

The distribution of calendar closing dates CCD (theoretical days of the year on which increment cycles were completed), was generated by converting closing dates into calendar days of the year.

Precision of age estimates

The otoliths from fish sampled in 1996 and 1997 ($n=972$) were read by the primary reader (reader 1) and by a secondary reader (reader 2). The primary reader also read the otoliths from fish sampled from 2001 to 2005 ($n=2450$). A random sample of around 25% of the otoliths sampled between 2001 and 2003 ($n=300$) were re-read by the primary reader and by another secondary reader (reader 3). The index of average percent error (APE) (Beamish and Fournier 1981) and age bias plots (Campana 2001) were calculated as indicators of ageing precision.

Bomb radiocarbon analysis

Following sample preparation procedures described in Kalish (1995a), and using juvenile otoliths and visible zones as a guide, a high speed hand-held drill was used to cut and grind outer material from the otoliths of seven adult fish, to leave material deposited in the first year of life. Resulting sample weights ranged from 1.4 to 4.2 mg. Otolith carbonate was converted to carbon dioxide by reaction *in vacuo* with 100% phosphoric acid. An aliquot of carbon dioxide was used to determine $\delta^{13}C$ for each sample and the remaining carbon dioxide was converted to graphite. Radiocarbon was determined in each graphitised sample by accelerator mass spectrometry (AMS) at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory (LLNL), University of California, or at the Radiocarbon Accelerator Unit, Research Laboratory for Archaeology and the History of Art (OxA), Oxford University. Radiocarbon values were reported as $\Delta^{14}C$, which is the age and fraction corrected deviation in parts per thousand from the activity of nineteenth century wood (Stuiver and Polach 1977) and were compared against the south-western Pacific calibration curve (Kalish 1993).

Growth modelling

Growth of the population sampled in 1996 and 1997 was described by sex using the von Bertalanffy growth function (VBGF). Initial inspection of the fit of the VBGF suggested that a fast initial growth phase and a slower subsequent growth phase were not well described, resulting in highly skewed residuals. Consequently, the generalised growth model of Schnute (1981) was also used to model growth:

$$L_t = L_{\infty}(1 + \alpha e^{-at^c})^{-\frac{1}{b}} + \varepsilon \quad (5)$$

where L_t is the length at age t ; L_{∞} is the asymptotic length; a , b , c and α are parameters of the function with b and c defining the shape of the function; and ε is a normal random residual error term with mean zero and standard deviation σ . Growth model parameters were estimated by maximising log-likelihoods assuming normally distributed residuals and gains in parsimony between the two growth functions were assessed using the Akaike Information Criterion (AIC) (Akaike 1974) and inspection of plots of residuals. The age estimates derived from counts of opaque zones for the juvenile sample were included in both the male and the female growth models to anchor the growth functions. The hypothesis of sexual dimorphism in growth was tested using a likelihood ratio test (LRT) (Kimura 1980). The juvenile sample was excluded from the male and female growth models used for this comparison.

Results

Otolith structure

When viewed with transmitted light at $25\times$ magnification, the transverse otolith sections showed alternating bands of translucent and opaque material radiating from an inner zone that was generally uniformly opaque (Fig. 1). Opaque and translucent zones adjacent to the inner zone were broad and decreased in width out to the growing edge. This reduction in width was rapid to around the fourth increment, after which consecutive increment cycles gradually narrowed in width out to the margin. Every otolith growing edge displayed a band of opaque material of around five microns wide, presumably from diffraction of light through structure damaged by the sectioning process. Otolith growing edges were interpretable out to around 10–15 increment cycles, after which the magnitude of optical artefacts regularly exceeded 25% of an increment cycle, obscuring the width of the last translucent zone. Interpretable otolith margins were generally wide for fish sampled between January and September inclusive ($>90\%$ wide and $<1\%$ narrow margins in each of these months). By contrast, in samples collected between October and December inclusive, margins were generally narrow ($>80\%$ narrow in each month).

Seventy-three otoliths (2.2% of the total examined) were rejected as a result of unclear increment structure or an inability to identify the primordium. Rejected otoliths were more or less evenly distributed among the years, regions, size range and sexes sampled.

Interpretation of inner structure

New settlers (45–75 mm FL) were easily recognised at the paper-fish stage owing to lack of pigmentation and were present in inshore reefs from early October, having spent approximately six months in the plankton (based on peak spawning in March and April) (Murphy and Lyle 1999). Fish sampled from the juvenile habitat throughout the year, and smaller fish from the gill-net samples, separated clearly into distinct size groups or cohorts (Fig. 2a). Fish lengths progressed from less than 80 mm in the new settlers (ns in Fig. 2a), to reach a mean of 132 mm ($n=5$) by the following March or April, at their first birthday (Fig. 2a).

Beyond this size, fish became increasingly furtive, making them difficult to hand-collect and resulting in small numbers of larger fish in the juvenile sample. Furthermore, in March and

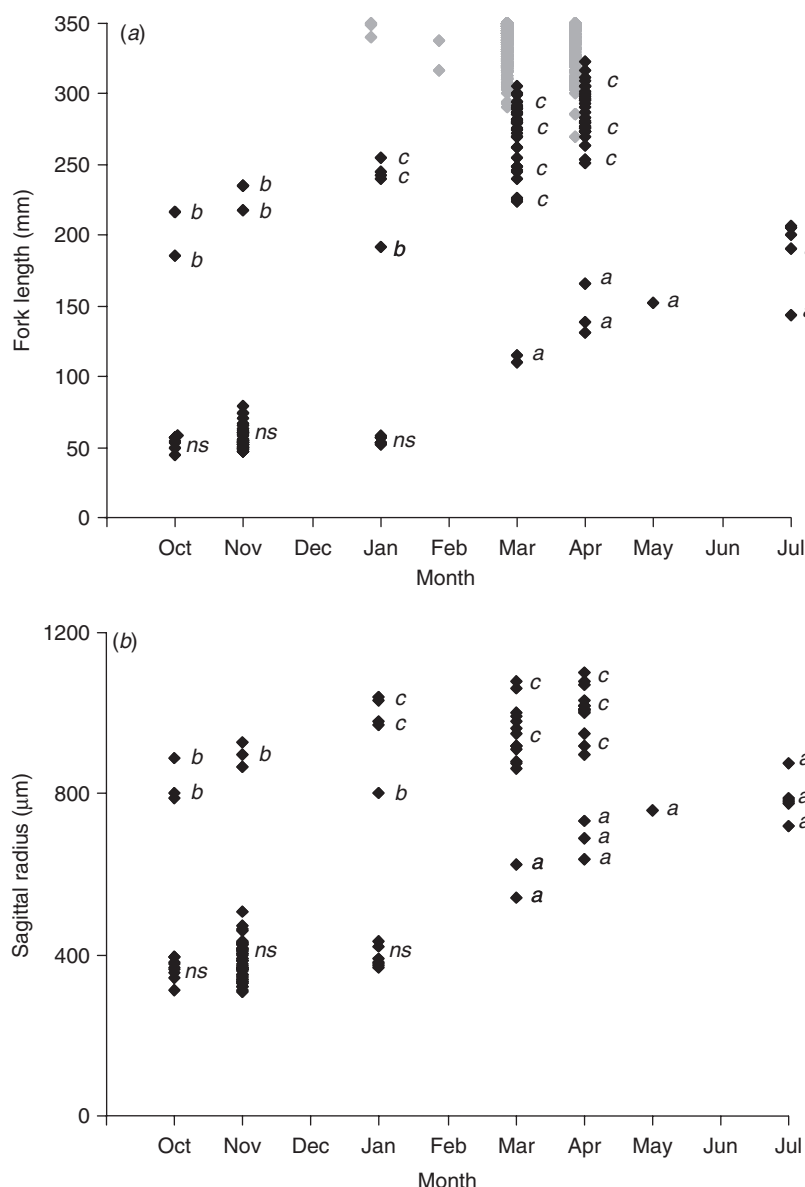


Fig. 2. Monthly progression of (a) length and (b) transverse radii of otoliths from juvenile *Cheilodactylus spectabilis*. Letter groupings refer to otoliths with similar visual characteristics to those displayed in Fig. 1 (*ns* refers to new settlers). The grey data points indicate fish with more opaque zones than group *c* otoliths and have been offset for clarity.

April there was a more or less continuous spread of sizes above 250 mm, reflecting the large sample sizes collected during the spawning season surveys (Fig. 2a). This, combined with increasing individual variation in size at age, promoted the risk of errors in a size based approach to ageing the juveniles. To minimise such errors, juvenile fish were assigned into groups on the basis of otolith structure. Excluding the new settlers (*ns* in Fig. 2), otolith sections separated clearly into three groups (*a*, *b*, *c* in Fig. 1), in addition to a group with more complex increment structure. Images of the otolith sections of the juvenile sample were then randomised and allocated to groups by readers 1 and 3 on the basis of otolith structure, with no reference to sample date or length or otolith radii measurements.

When referenced to sample date it became apparent that group *a*, with a large and distinctive translucent zone (T1) on the margin (Fig. 1), matched the smaller (110–207 mm) of the two size classes present between March and July (Fig. 2a). This translucent material was presumably deposited in their first summer. Group *b* had opaque material present on the growing edge exterior to T1, and represented the larger size class (185–235 mm) present in October and November, with one individual also present in January (Fig. 2a). Group *c* had translucent material on the growing edge (T2), preceded by a distinctive opaque zone (O1), and was present between January and April, ranging between 224 and 323 mm in length. Presumably, O1 was deposited in the second winter and/or spring and was followed

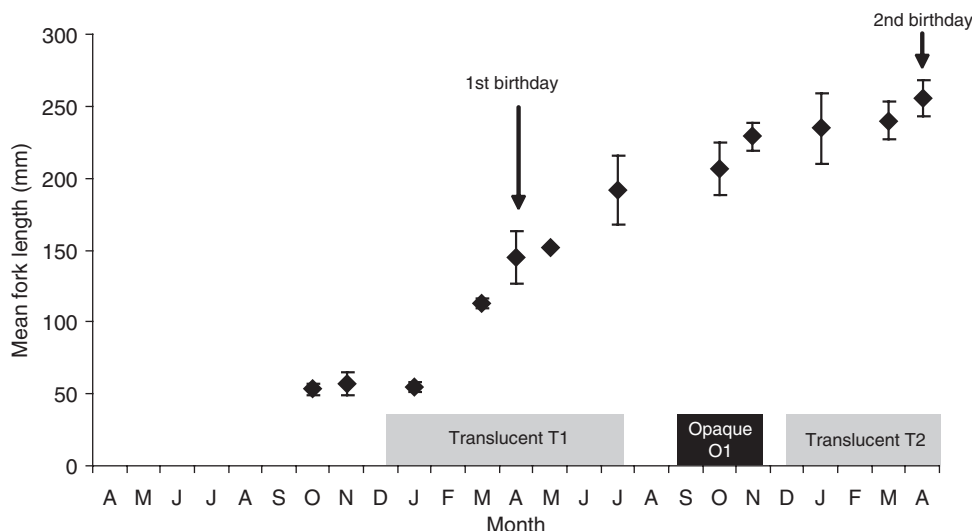


Fig. 3. Monthly progression of mean fork length of juvenile *Cheilodactylus spectabilis* showing the sequence of otolith groups (refer Fig. 1) and related zone formation at the otolith growing edge. Error bars are standard deviation.

by translucent material from the second summer of growth (Fig. 3).

The grey data points in Fig. 2a, included all otoliths with more opaque increment structure beyond O1. Ignoring this fourth and presumably older group, the separation between the new settlers and fish at 18 months old (groups *ns* and *b*) and the separation between fish sampled around their first and their second birthdays (groups *a* and *c*) became clear. Under this interpretation of cohort structure (Fig. 3), juveniles had reached mean lengths of 186 mm ($n = 7$) by their second winter (July, at around 15 months old), 217 mm ($n = 6$) by the following spring (October and November, at around 19 months old), and 248 mm ($n = 28$) by their second birthday in March and April. The plot of otolith radii against sample month (excluding the grey data points in Fig. 2a) showed the same cohort structure (Fig. 2b).

Visual and dimensional examination of otolith sections from adults revealed that the features T1, O1, and scalloping on the distal growing edge (adjacent to T1), were distinguishable in every readable section (Fig. 1). Further, O1 was dimensionally stable (mean transverse radius of 770 μm ($n = 100$, $se = 2.1$)) in adult sections and was consistent with the mean transverse otolith radius of juveniles in their second winter (783 μm ($n = 7$, $se = 17.6$)). The region inner to T1 was referred to as the inner zone. In a small proportion of otoliths, one or more translucent zones were visible in the inner zone, presumably owing to lower section thickness. However, in every case this inner zonation was elliptical around the primordium rather than terminating in scalloping on the distal growing edge and therefore could not be confused with T1. Consequently, O1 was selected as the first opaque zone in counts for the purposes of age estimation and was arbitrarily dated at 1 October (i.e. equivalent to 1.5 years of age) (Fig. 3).

Periodicity and timing of opaque zone formation

Of 94 OTC tag-recaptures, 29 had been at liberty for more than 200 days and displayed an unambiguous fluorescent mark in their

otoliths. Twenty-six of these were suitable for the methodology described by Cappo *et al.* (2000) to measure the periodicity of opaque zone formation. These fish ranged in estimated age from five to 73 years, with times at liberty of between 0.65 and 8.29 years (Table 1). The three otoliths that were excluded from this method had fewer than five increment cycles and consequently failed the assumption that increment cycles in the vicinity of the margin were of equal width. These otoliths, did however display the expected number of increment cycles to support annual deposition of opaque zones in late winter. The higher magnification (100 \times) used for the measurement of partial increment cycles to calculate the liberty fraction (*LF*), decreased the width of the optical artefact at the growing edge of otoliths sufficiently for these measurements to be taken on otoliths from all of the fish in the OTC sample.

A significant linear relationship ($F_{25} = 999$, $P < 0.001$), with a slope of 0.97 (95% confidence interval 0.91–1.03) and an intercept of -0.04 (95% confidence interval -0.27 to 0.19), existed between the liberty fraction (*LF*) and time at liberty (*L*) (Fig. 4). There was no significant relationship between the residuals of the number of increment cycles formed outside the OTC mark and time at liberty ($F_{25} = 0.03$, $P = 0.85$). Over 88% of whole year counts of increments between the OTC mark and the growing edge agreed with whole years at liberty and no counts were different by more than one year. Over 85% of the CCDs fell in the months from June to December (inclusive) indicating that opaque zones were most likely to be completed in that period (Fig. 5).

Assignment of ages from increment counts

Counts of opaque zones were commenced from and included O1, and proceeded to the proximal margin adjacent and ventral to the sulcus acusticus (Fig. 1). For the purposes of age estimation, only readable otoliths from fish collected in the months of April and March (around 3200) were used. Other months were excluded to

Table 1. Estimated age at recapture, number of opaque zones exterior to the oxytetracycline (OTC) mark, time at liberty and calculated liberty fraction (LF)

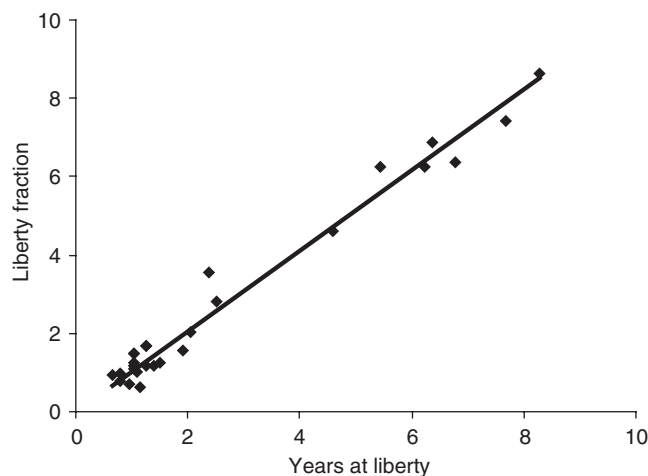
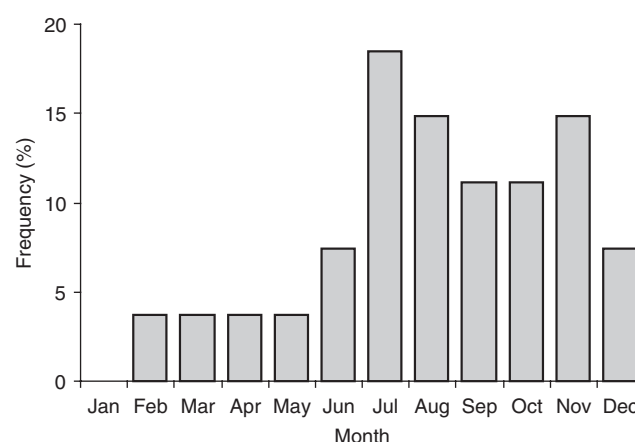
Age estimate	Number of opaque zones	Time at liberty (years)	LF
8	0	0.65	0.95
4*	0	0.69	–
15	0	0.80	0.99
71	0	0.80	0.78
5	0	0.95	0.70
5	1	1.03	1.24
62	1	1.05	1.08
7	1	1.05	1.18
58	1	1.05	1.49
9	1	1.05	1.49
6	0	1.15	0.62
4*	1	1.22	–
7	1	1.25	1.18
6	1	1.25	1.68
31	1	1.25	1.68
39	1	1.40	1.18
6	1	1.50	1.25
41	1	1.90	1.56
8	2	2.05	2.03
2*	2	2.16	–
22	3	2.38	3.57
9	2	2.52	2.81
13	4	4.60	4.63
10	6	5.43	6.25
11	6	6.23	6.25
15	6	6.38	6.87
73	6	6.78	6.39
24	7	7.68	7.43
26	8	8.29	8.62

*Fish excluded from the OTC model.

ensure that variation in the timing of detection of newly deposited opaque zones, around the time of opaque zone formation, did not lead to ageing errors. More than 99% of the otoliths in this restricted adult ageing dataset displayed either a medium or a wide translucent margin and any opaque material evident on a margin was ignored in enumeration. Counts were converted to ages using the following formula:

$$t = (\text{count} + 0.5) + (t_{\text{cap}} - \text{CCD}_{\text{arb}}) \quad (6)$$

where t is the age estimate, count is the number of opaque zones plus 0.5 years to correct for the age at O1, t_{cap} is the capture date and CCD_{arb} is the theoretical calendar closing date of the last enumerated opaque zone. The difference between t_{cap} and CCD_{arb} is expressed as a fraction of a year and is added to the age estimate to account for the time elapsed between the date of capture and the last enumerated opaque zone. CCD_{arb} was set arbitrarily as the 1st of October immediately before the capture date. This date was chosen as it fell within the range of months with a high proportion of calendar closing dates and complemented the date chosen for O1.

**Fig. 4.** Estimated liberty fraction plotted against time at liberty for *Cheilodactylus spectabilis* marked with oxytetracycline (OTC). The regression line is shown.**Fig. 5.** Monthly percentage frequency of calendar closing dates of the last complete increment cycle for *Cheilodactylus spectabilis*.**Table 2.** Average percent error (APE) values for within and between reader comparisons for all ages and for fish of estimated ages of 60 years or more

Comparison	Reader 1 (all ages > 60 years)
Reader 1	1.1/1.5
Reader 2	1.78/1.1
Reader 3	1.8/1.99

Precision of age estimates

APE scores for within and between reader differences all lay below 2% (Table 2), with no obvious evidence of bias apparent in age bias plots. Despite the possibility that ageing differences may be higher among older fish, APE scores were still low for fish greater than 60 years of age (Table 2).

Table 3. Radiocarbon and otolith-based age data

Errors in $\Delta^{14}\text{C}$ are standard deviations; LLNL, Lawrence Livermore National Laboratory; Radiocarbon Accelerator Unit, Research Laboratory for Archaeology and the History of Art (OxA), Oxford University

Otolith-based age data		Laboratory	Radiocarbon data	
Age estimate	Birth year		Sample weight (mg)	$\Delta^{14}\text{C}$ (‰)
54	1940	LLNL	2.3	-66.6 ± 7.7
37	1957	LLNL	2.1	-45.8 ± 8.0
32	1962	OxA	4.2	-30 ± 9.0
16	1978	OxA	1.9	84 ± 8.0

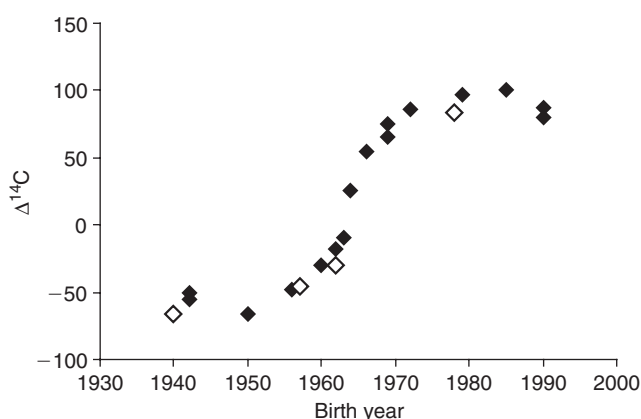


Fig. 6. Radiocarbon values reported as $\Delta^{14}\text{C}$ ‰ and plotted against birth year. Open symbols represent *Cheilodactylus spectabilis* with birth year derived from counts of otolith annuli, closed symbols represent the South Western Pacific calibration, which is provided by $\Delta^{14}\text{C}$ data from age validated *Pagrus auratus*.

Bomb radiocarbon analysis

Of the seven otolith samples that were prepared, three were unusable as a result of unsuccessful preparation of the graphite target, contamination or poor precision. Radiocarbon measurements of the four successful samples are presented in Table 3, and when plotted against birth date estimates derived from counts of otolith opaque zones, were consistent with the increase in bomb-derived radiocarbon concentrations from the south-western Pacific calibration curve (Fig. 6). The fish with an otolith age estimate of 32 years, and an otolith birthyear of 1962, was born during the period of rapid increase in radiocarbon that occurred between 1960 and 1974 and from the calibration curve had a radiocarbon chronometer birth year of 1961 ± 2 . The fish with an otolith age estimate of 37 years, and an otolith birthyear of 1957, had a radiocarbon concentration consistent with the pre-bomb era and confirms that *C. spectabilis* live to at least 37 years of age. The fishes aged at 54 and 16 years have birthdates well outside the period of rapid increase in bomb radiocarbon and although consistent with the calibration curve, do not contribute to the examination of the accuracy of otolith age estimates.

Growth modelling

Maximum assigned ages for females and males were 94 and 97 years respectively. For growth modelling, only fish sampled from 1996 to 1997 were used; the oldest female and male being 86 and 81 years respectively (Fig. 7). The Schnute and Richards generalised growth model produced a more even distribution of residuals than the VBGF for both males and females. Values for the AIC for females were 4187 and 4425 and for males were 2633 and 2757 for the generalised growth model and the VBGF respectively. The generalised growth model parameters for females were: $L_{\infty} = 432.7$, $a = 22.6$, $b = 2.7 \times 10^{-8}$, $c = 0.02$, $\alpha = 219.6$ and for males were: $L_{\infty} = 550$, $a = 7.7$, $b = 2.8 \times 10^{-6}$, $c = 0.1$, $\alpha = 0.01$ (Fig. 7). The LRT between the growth functions for females and males indicated significant differences on every comparison except the α parameter constraint (coincident curves constraint: $\chi^2_5 = 930$, $P < 0.001$).

Discussion

A robust validation protocol should include an estimate of the age at the first enumerated zone (Campana 2001). Through the use of fish length in conjunction with otolith structure we were able to age the juvenile sample and hence assign an age of 18 months to the first enumerated zone (O1) in adult *Cheilodactylus spectabilis* otolith sections. Despite the distinctive appearance and position of this zone, there was evidence in some otoliths of complex incremental structure deposited before O1. Through understanding the timing and appearance of the otolith inner structure we have been able to identify such sub-annual increment structure which, if counted, would overestimate age.

Validation should also include estimation of the periodicity and timing of increment formation (Campana 2001). The most commonly used methods to satisfy this requirement involve examination of the otolith growing edge and require samples collected at regular intervals within years and ideally over an extended period (at least 2 years) and should be replicated across age classes. For long-lived species, such as *C. spectabilis*, such methods can be problematic because the narrow increment structure at the growing edge of older individuals makes interpretation of the margin type uncertain and regular samples from numerous age classes require very large sample sizes. The OTC mark-recapture technique reduces the requirement for sampling all age classes as periodicity is estimated over the entire period at liberty for each fish. The quantitative OTC model (Cappo *et al.* 2000) confirmed that opaque zones were deposited annually across a wide range of age classes in *C. spectabilis*.

In relation to the timing of increment formation, the broad peak in the distribution of calendar closing dates predicted by the OTC model suggested that opaque zones may have closed as early as June and as late as December. However, as the model detects closing dates on the basis of ratios of increment widths, the annual pattern of wide and narrow translucent margins, recorded for the sections viewed under low magnification, suggest that this conclusion may be misleading. Under low magnification, the opaque optical artefact on the growing edge obscured the formation of opaque zones, which were only detectable after the onset of translucent zone formation on the otolith growing edge. As narrow translucent margins were

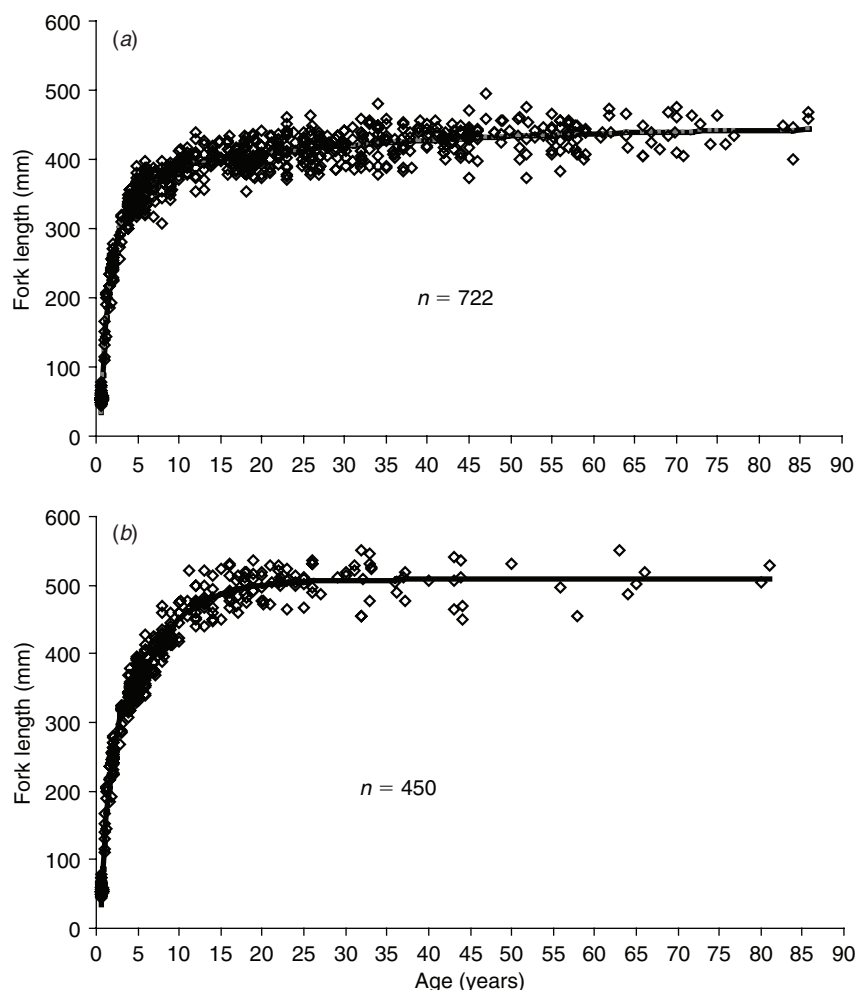


Fig. 7. Length at age data for (a) female and (b) male *Cheilodactylus spectabilis* with data and fitted Schnute generalised growth models (black lines).

only observed for a short period (October–December) and wide translucent margins were dominant for the remainder of the year, it can be inferred that otolith growth was rapid during the formation of translucent material after which otolith growth slowed until the following spring. Despite the model being unable to detect whether or not a wide margin terminated in an opaque zone at the growing edge, it was able to accurately predict the cessation of opaque zone closures (in December). Thus, it is likely that opaque material is deposited in the late austral winter and early spring, at the end of an extended period of slow otolith growth. This timing is consistent with that of the juvenile sample and is also consistent with the timing of opaque zone formation in several other species from the region (Ferrell *et al.* 1992; Fowler and Short 1998; Gillanders *et al.* 1999; Stewart *et al.* 1999; Ewing *et al.* 2003; Smith and Deguara 2003).

As a result of variation in the ability to detect newly completed opaque zones on the growing edge around the time of opaque zone formation, there is potential for individuals of a given age group to be assigned to different ages classes when sampled during such times (Francis *et al.* 1992; Ewing *et al.* 2003; Smith and Deguara 2003). This variation could result from variation

in section quality (a wider optical artefact on the margin may delay detection), individual variation in otolith growth rate, and individual variation in the timing of opaque zone completion (Stewart *et al.* 1999). Methods of dealing with this problem range from restricting age estimation to fish collected outside the time of annulus formation (Francis *et al.* 1992; Smith and Deguara 2003), to the generation of algorithms to infer the presence of unseen annuli on the margin (Francis *et al.* 1992; Fowler and Short 1998; Ewing *et al.* 2003). In the present study, we have adopted the former approach, with age estimates restricted to fish collected in March and April.

The biological processes that govern the deposition of annuli in otoliths have been the focus of considerable discussion (Beckman and Wilson 1995), with annulus deposition related to annual migrations (Tserpes and Tsimenides 1995; Franks *et al.* 1999) and the timing of spawning (Hostetter and Munroe 1993; Ferreira and Russ 1994). Such factors are unlikely to influence opaque zone formation in *C. spectabilis* because they are home-ranging (McCormick 1989b; Murphy and Lyle 1999) and opaque zones are formed at a similar time of the year in adults and juveniles. Otolith growth has also been linked

with environmental events, particularly temperature variation (Lombarte and Leonart 1993; Woodbury 1999). Our estimate of the timing of the opaque zone formation in *C. spectabilis* is coincident with a steep increase in sea surface temperatures (SST) on the south-east Tasmanian coast, from a long-term annual mean minima of 12.6°C (s.d. = 0.44) in August, to a mean of 15.2°C (s.d. = 0.88) in December and to a mean annual maximum of 17.1°C (s.d. = 0.83) in February (SST data sourced from NOAA-CIRES Climate Diagnostics Center, Boulder, CO 80305, USA).

Although OTC mark-recapture techniques are particularly useful for long-lived species such as *C. spectabilis*, they do not provide a measure of absolute age, since the increment structure before capture is not validated. The bomb radiocarbon analyses provided a temporal reference point that confirmed that our otolith-based age estimates were accurate to within 2 years at 32 years of age, that *C. spectabilis* live beyond 37 years of age, and supported the notion that our age estimates were accurate above and below these ages. *Cheilodactylus spectabilis* were well suited for the bomb radiocarbon chronometer because they are long-lived (with estimated birthdates before the increase in bomb radiocarbon), and they are known to inhabit well mixed surface waters during their first year of life (Wolf 1998; Bruce *et al.* 2001). The calibration curve proposed by Kalish (1993) is suitable for comparison with *C. spectabilis* because the species used to derive the curve, *Pagrus auratus* sampled off the north-east coast of New Zealand, are also from well mixed surface waters of the south-western Pacific Ocean. This is further supported by close agreement between the calibration curve and radiocarbon values for *Centroberyx affinis* (Kalish 2001), sampled from the coastal shelf waters on the south-east coast of Australia.

Cheilodactylus spectabilis exhibited an unusual combination of rapid initial growth and extreme longevity, with growth trajectories for both sexes characterised by individuals reaching the asymptotic size at around 15 years of age, i.e. less than 20% of the maximum age recorded. The standard VB growth function poorly described this growth pattern, with unrealistically low initial growth rates and an underestimation of the asymptotic length. The generalised growth model of Schnute (1981) provided a more even distribution of residuals and more realistic asymptotic lengths. There was also substantial and statistically significant sexual dimorphism in the asymptotic lengths achieved by *C. spectabilis*; no females were encountered that even reached the male asymptotic length. The co-gener *C. fuscus* occurs on the south-east Australian coast (Gomon *et al.* 1994) and is also relatively long-lived, with a maximum recorded age of 40 years (Lowry 2003), and has similar sexual dimorphism with males attaining generally larger sizes than females (Schroeder *et al.* 1994).

Fish exhibiting extreme longevity tend to be deep water species (Cailliet *et al.* 2001). *Cheilodactylus spectabilis* appears to be an exception, restricted to depths of less than 50 m (Gomon *et al.* 1994). A review of records in the MATURITY table of the Fishbase Database (Froese and Pauly 2006) for species that live in excess of 60 years yielded 27 exclusively marine species, of which only one other species (*Stereolepis gigas*) (Eschmeyer *et al.* 1983), also resides in shallow waters of less than 50 m. Longevity and age at maturity in fishes also tend to be correlated and Froese and Binohlan (2000) have developed an empirical

relationship based on over 400 species to describe this association. With age at maturity of just 4 years (Murphy and Lyle 1999) *C. spectabilis* is an outlier, falling approximately twice as far as the maximum residual from the expected logarithm of age at maturity described by the longevity and maturity relationship. Furthermore, of the species in the Fishbase MATURITY table for which age at maturity is available, the average age at maturity for those whose lifespan exceeds 60 years is 14.4 years, with most maturing at over 10 years of age and no other species maturing at 4 years or less. The ecological significance of this life history strategy warrants further attention.

In summary, the quantitative approach to OTC tag-recaptures and the bomb radiocarbon methods complemented each other by providing a measure of absolute age, estimating periodicity over a large number of years of otolith growth and giving accurate measures of periodicity and timing of zone formation. This, combined with an understanding of the age of inner otolith structures and avoiding periods when outer otolith structure may be ambiguous, has promoted the likelihood of achieving accurate estimates of age and growth for this species.

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