Life-history traits of the leatherjacket *Meuschenia scaber*, a long-lived monacanthid

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The present study describes the age and growth of the leatherjacket *Meuschenia scaber*, a common Australasian monacanthid and valued by-catch of the inshore bottom trawl fishery in New Zealand. Age was determined from the sagittal otoliths of 651 individuals collected between July 2014 and March 2016 in the Hauraki Gulf of New Zealand. Otolith sections revealed alternating opaque and translucent zones and edge-type analysis demonstrated that these are deposited annually. *Meuschenia scaber* displayed rapid initial growth, with both males and females reaching maturity in 1–2 years and 50% of both sexes matured at 1·5 years. Maximum age differed substantially between the sexes, at 9·8 years for males and 17·1 years for females. Growth rate was similar between sexes, although males reached greater mass at age than females in the early part of the lifespan. The length–mass relationship differed significantly between the sexes, with males displaying negative allometric growth and females isometric growth. Female condition was highest in July, declined in August with the onset of spawning and showed a slight peak in January and February, immediately following the spawning season. This study substantially extends the maximum longevity recorded for monacanthids, although males had much shorter lifespans and higher mortality, than females.

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Key words: age; age at maturity; growth; Monacanthidae; mortality; otolith.

INTRODUCTION

Life-history characteristics have been described for many exploited reef-associated fishes (*e.g.* parrotfish, groupers), providing estimates of growth, lifespan, reproduction and mortality parameters (Choat & Robertson, 2002). An understanding of age-based life-history traits is critical for the development of conservation and management strategies. For example, knowledge of life-history traits allows fishery managers to model population dynamics of stocks and to determine regulations (*e.g.* mesh size, size limit and total allowable catches) (Adams, 1980; King & McFarlane, 2003).While such data are available for many valued commercial species, understanding of demographic parameters remains limited for many non-target fish taxa.

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The Suborder Balistoidei comprises over 149 species and includes the triggerfishes (Balistidae) and filefishes (Monacanthidae), which are found in tropical and subtropical regions worldwide (Matsuura, 2015; Nelson *et al.,* 2016). Current knowledge of the life history of monacanthids is based on a few species of commercial value that have relatively short lifespans and indeterminate growth patterns (Hutchins, 1999; Miller, 2007; Shepherd & Edgar, 2013). Ecological and evolutionary interest in studying monacanthid life-history traits arises from two aspects of their biology: they are very diverse in southern Australasian waters, with over 20 species only occurring in temperate reef habitats in southern Australia and over 32 genera in Australian waters as a whole (Gomon *et al.,* 2008); they appear to feed selectively on benthic reef biota, with some species having profound effects on these biota by removing a significant biomass of sponges, ascidians and bryozoans from reef surfaces at intermediate depths (Ayling, 1981).

Age and growth estimation of monacanthids has been based mainly on counting growth increments in the anterior dorsal spine or in the vertebrae. Ageing studies on the anterior dorsal spine of *Stephanolepis hispidus* (L. 1766) in the Canary Islands (Mancera-Rodríguez & Castro-Hernández, 2004) and *Stephanolepis diaspros* Fraser-Brunner 1940 in the Gulf of Suez (EL-Ganainy *et al.,* 2008) yielded maximum ages of three and four years, respectively. The use of vertebrae for ageing monacanthids such as *Thamnaconus modestus* (Günther 1877) in Korean waters, including Jeju Island, (Park, 1985; Kim *et al.,* 2016) and *Nelusetta ayraud* (Quoy & Gaimard 1824) in the eastern waters of the Great Australian Bight (Grove-Jones & Burnell, 1991), also yielded to short lifespan estimates (<9 years). Miller *et al*. (2010) recently reviewed otolith-based age estimation for *N. ayraud* and emphasized however, the limited precision and accuracy of previous results based on age estimation using vertebrae. Otolith-based studies have also been successfully conducted on early life stages and juveniles of *S. hispidus* (Rogers *et al.,* 2001), *Rudarius ercodes* (Jordan & Fowler 1902) and *Paramonacanthus japonicus* (Tilesius 1809) (Kawase & Nakazono, 1994) and *Monacanthus tuckeri* (Bean 1906) (Ben-David & Kritzer, 2005). Annual increment deposition has been reported in sagittal otoliths of the monacanthid species *Meuschenia australis* (Donovan 1824)*, Penicipelta vittiger* (Castelnau 1873) and *N. ayraud* (Barrett, 1995*;* Miller *et al.,* 2010), suggesting that this pattern occurs generally in the group.

The leatherjacket *Meuschenia scaber* (Forster 1801) is commonly found in temperate Australasian waters and is the most abundant member of the Monacanthidae in New Zealand (Francis, 1996). It inhabits a wide depth range from shallow waters down to 100 m and is a valuable by-catch of inshore bottom trawl fisheries in New Zealand. Despite increases in demand and market value in recent years (Raje, 2016), little is known of the life history or population dynamics of this species and science-based management has therefore not been possible. Kingsford & Milicich (1987) used otoliths to determine the growth of pre-settlement phase *M. scaber* younger than 66 days and Poynter (1980) studied growth in length, based on a tag–recapture study on shallow reefs in north-eastern New Zealand and conservatively estimated maximum age to be 5 years. It is not possible, however, to accurately determine maximum age of bony fish from mark–recapture and underestimating age will result in an overestimate of productivity and therefore poor management advice.

Meuschenia scaber is the only species in New Zealand waters documented to base its diet on encrusting animals such as sponges, ascidians, echinoderms, polyzoans,

hydroids and barnacles (Russell, 1971). In addition, the study species recruits preferentially into the canopy and fronds of *Ecklonia radiata*, a laminarian alga that undergoes massive temperature-mediated die-offs over large areas of reef habitat (Choat & Ayling, 1987). Given the ecology and feeding biology of *M. scaber*, the nature of growth and mortality variables is of considerable interest. Fisheries management is strongly influenced by mortality and age at maturity of the target species. Long-lived species, especially those which show limited somatic growth and reproductive outputs after achieving an asymptotic size, are generally prone to overfishing (Choat & Robertson, 2002). In addition, the nature of their effect on the benthic biota makes the stability of adult populations a matter of considerable interest. Thus, for this group, which is increasingly targeted by fisheries (FAO, 2006), estimates of growth profiles, reproductive outputs and longevity are of interest in the context of both fisheries management and ecological interactions.

Accordingly, the focus of this study was the provision and analysis of age-based life-history data necessary to determine maximum age, growth, age at maturity, natural mortality and condition of *M. scaber* in the Hauraki Gulf.

MATERIAL AND METHODS

SAMPLE COLLECTION

A total of 651 *M. scaber* was collected in the Hauraki Gulf (35·9–36·6° S; 174·7–175·9° E) on the north-eastern coast of the North Island of New Zealand. Monthly samples totalling 499 specimens were caught by underwater spear-gun between July 2014 and March 2016 on shallow reefs (0–12 m). Samples were selected randomly with regard to length within each sex. These samples were supplemented with 152 individuals taken by commercial trawlers in the Hauraki Gulf (40–53 m depth) over the same time period. In addition, 20 juveniles of *M. scaber* (<110 L_T mm) were collected by hand spear in February 2015 and January 2016.

Total length (L_T) and standard length (L_S) were recorded for each fish to the nearest mm and total mass (M_T) and gutted mass (M_{Gut}) to the nearest mg. Each fish was sexed, assigned a macroscopic maturity stage (Visconti *et al.*, 2017) and the extracted pairs of sagittal otoliths were rinsed in 70% ethanol and stored dry in 96-well plates.

OTOLITH PREPARATION AND AGE DETERMINATION

Age determination was based on thin transverse sections of sagittal otoliths (Secor *et al.*, 1995; Trip *et al.*, 2011*a*). One of each pair of otoliths [Fig. 1(a)] was randomly selected and weighed to the nearest mg prior to mounting on a glass slide with thermoplastic cement (Cristalbond, Triangle; www.celmac.com.au) for grinding. Each otolith was ground from the posterior and anterior margins to obtain a thin transverse section through the nucleus using a diamond polish wheel with a P1200-grade wet and dry sandpaper. Otoliths from juveniles (82–108 L_T mm) were polished by hand using 3 and 1 μm aluminium oxide lapping film.

Otoliths from juvenile individuals (<1 year, sagittal otolith mass < 300 mg) were aged using daily increments (in days) with ImageJ (www.imagej.nih.gov) and ObjectJ (www.simon.bio.uva.nl/object) software and used to ensure that the position of the first
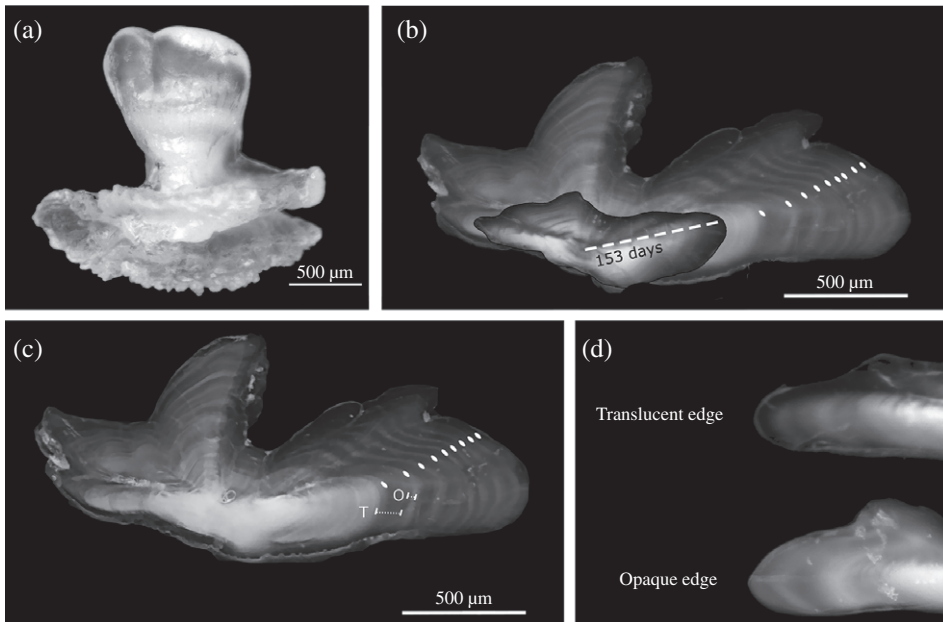
Fɪɢ. 1. *Meuschenia scaber* (a) whole otolith; (b) a 153 day-old otolith overlaying a 9 year-old otolith showing the position of the first annual growth check; (c) thin transverse section of an adult otolith showing age counts with opaque zone (O) and translucent zone (T); (d) a comparative image of an opaque edge *v*. a translucent edge.

annual check was not hidden in the core area [Fig. 1(b)]. Juvenile otolith sections were viewed under transmitted light with a compound microscope at ×100 magnification. One daily increment was defined as the combination of one opaque and one translucent zone. The precision of readings was checked by examining the correlation between otolith mass and the number of increments, on the assumption of a linear increase in otolith mass with age (Boehlert, 1985; Pawson, 1990; Fletcher, 1991; Francis *et al.,* 2005).

Prepared adult otoliths were viewed with a Leica M80 stereomicroscope (www.leica .com) at ×6·5 magnification against a black background and under reflected light. Digital images were captured for further analyses [Fig. 1(c)]. The otoliths sections showed a clear pattern of alternating opaque and translucent zones [Fig. 1(c)] and the periodicity and timing of opaque-zone formation in *M. scaber* was investigated using edge-type analysis (ETA) [Fig. 1(d)], whereby the monthly proportion of otoliths with opaque margins (pooled across like months) were plotted (Manickchand-Heileman & Phillip, 2000; Ewing *et al.,* 2004; Pears *et al.,* 2006).

Each otolith section was read three times by the first author (V.V.); counting the number of opaque zones, without any reference to length. When all three counts were identical, the reading was taken as the final estimate of age; when two out of the three readings coincided, the coinciding value was taken as the final age estimate. When readings deviated by more than 1 year, a fourth reading was taken. If the reading coincided with any of the previous readings that value was taken as the final age estimate, otherwise the individual was not included in the age-based analyses.

Decimal age was calculated for each fish based on the number of opaque zones and timing of deposition, the sample date and a nominal birth of 1 October; which is the mid-point of the spawning season in the Hauraki Gulf (Visconti *et al.*, 2017).

In order to examine the precision of the reading, the C.V. and the average percentage error ($\bar{E}\%$) were calculated among readings. APE was calculated following Beamish & Fournier (1981): $\bar{E}_J\% = 100\{R^{-1}\sum_{i=0}^{R}[\,(|X_{ij} - X_j|)X_j^{-1}]\}$, where R is the number of times each fish is aged, X_{ij} is ith age determination of the jth fish and Xj is the mean age calculated for the jth fish.

The C.V. was estimated from the average C.V. across all individuals aged and expressed as follows: $(\text{C.V.})_j = 100\langle\{\sqrt{\left[\sum_{i=1}^{R}\left(X_{ij}-X_j\right)^2(R-1)^{-1}\right]}\} \ X_j^{-1}\rangle$, where $(\text{C.V.})_j$ is the coefficient of variation of age readings for fish j, Xij is the ith age reading for fish j, Xj is the mean age estimate across all readings and R is the number of readings (Campana, 2001).

GROWTH PARAMETERS

The reparameterized von Bertalanffy growth function (rVBGF; Francis, 1988) was fitted to the length-at-age data for *M. scaber*, for the sexes combined and for females and males, separately. The rVBGF is based on three parameters, L_τ, L_ω and L_μ, which express expected average body length at three arbitrary ages τ, ω and μ. The rVBGF equation is as follows: $L_t = L_\tau + \langle\{(L_\mu - L_\tau)\,1 - \text{r}[2(\text{t} - \tau)(\mu - \tau)^{-1}]\}(1 - r^2)^{-1}\rangle$, where $r = (L_\mu - L_\omega)(L_\omega - L_\tau)^{-1}$ and L_t is the average length at age to be predicted by the model. Ages τ and μ were chosen as the most representative ages in the dataset for *M. scaber* and age ω was calculated as the average of τ and μ. Age τ was chosen to reflect the ascending part of the growth trajectory (*i.e.* the period of fast, early growth, $\tau = 1$), age μ to represent the asymptotic part of the curve (*i.e.* when growth reach the plateau, $\mu = 5$) and age ω reflected the onset of a reduction in growth rate ($\omega = 3$). The rVBGF was fitted by constraining the curve to a length at settlement of 10 mm L_T (Kingsford & Milicich, 1987). The best-fit model parameters, L_1, L_3 and L_5, were estimated by minimizing the negative natural log of the likelihood and assuming a normal probability distribution of the residuals, with mean L_t and standard deviation σ (Haddon, 2001). The standard VBGF parameters L_∞ (mean asymptotic size), K (curvature parameter) and t_0 (age at which the fish have a theoretical size of zero) were also derived following Francis (1988) for both females and males of *M. scaber*.

In addition, and because male and female *M. scaber* have different length–mass relationships, the von Bertalanffy growth function was fitted to the mass-at-age data for each sex following the formula: $M_t = M_\infty[1 - \exp(-K(t - t_0))]^3$, where M_t is the gutted mass (M_{Gut}) at age t; M_∞ is the mean asymptotic mass, K the curvature parameter and t_0 is age at which the fish have a theoretical mass of zero. Likelihood ratio tests were used to statistically compare fitted growth curves for males and females, as well as the following VBGF parameters: L_∞, K, $t_0\ L_1$, L_3, L_5 for growth in length; and $M_{\infty,}$ K and t_0 for growth in mass (Kimura, 1980; Cerrato, 1990; Haddon, 2001).

LENGTH–MASS RELATIONSHIP AND CONDITION

The relationship between length and mass of *M. scaber* females and males was described with the following equation: $M_T = aL_T^b$, where M_T is the total mass, a

(y-intercept), L_T is the total length and b (slope) is the growth coefficient. This formula was transformed into its linear form as: $\log M_T = \log a + b \log L_T$. The 95% C.I. was calculated for both a and b parameters and an analysis of covariance (ANCOVA) was used on the transformed (linear) data to test for differences in the length–mass relationship between the sexes.

The relative condition factor was calculated for *M. scaber* as a monthly mean based on Le Cren's (1951) equation and following Griffiths (2002): $K_{nj} = \left\{ \sum_i^n \left[Mi \left(aL_{Ti}^b \right) \right] \right\} n_j^{-1}$, where K_{nj} is the monthly relative condition, M_i is gutted mass (M_{Gut}) of the ith individual in the jth month; L_{Ti} is the total length (mm) of the ith individual; a and b are the constants from the length–mass relationship based on gutted mass (present study); n_j is the number of fish sampled in the jth month.

AGE AT MATURITY

The age at sexual maturity (T_{50}) of *M. scaber* was determined using females and males collected during the spawning season based on reproductive categories in Visconti *et al*. (2017). Age at maturity was estimated from the age at which 50% of females or males were sexually mature (T_{50}) following Williams *et al*. (2008) and Trip *et al*. (2011*b*). The logistic function (the maturity ogive) was fitted to the proportions of mature fish in each year class that were sampled during the spawning season and the ogive was fitted to the mid-point of each age class. The best-fit logistic function was estimated by minimizing the negative $\log_{10}$ of the likelihood based on a probability density function with a binomial distribution (Haddon, 2001). A bootstrapping procedure was used to estimate 95% C.I. (Moore *et al.,* 2007) from the 2·5 and 97·5 percentiles of the bootstrap estimates (Haddon, 2001). A likelihood-ratio test was used to test for differences between males and females.

MORTALITY

Rates of instantaneous total mortality (Z) for female and male *M. scaber* were derived from age-based catch curves. The natural logarithm of the frequency of sampled individuals per age class was plotted against corresponding ages (years). Z was calculated as the absolute value of the slope of a line ($y = mx + b$) fitted to the descending limb of the curve (Beverton & Holt, 1957). Rates of total mortality for males and females were also estimated using the Chapman-Robson method (1960) (CR) method (Chapman & Robson, 1960).

RESULTS

PERIODICITY AND TIMING OF OPAQUE-ZONE FORMATION: VALIDATION OF ANNUAL INCREMENTS

The ETA performed on 651 *M. scaber* otoliths revealed a clear periodicity in alternating opaque and translucent zones. From November 2014 to July 2015 and including July 2014, the proportion of otoliths with an opaque zone was <50%. On the other hand, a peak of opaque zone presence was recorded from late winter through the austral spring, between August and October 2014, with more than 50% of individuals showing
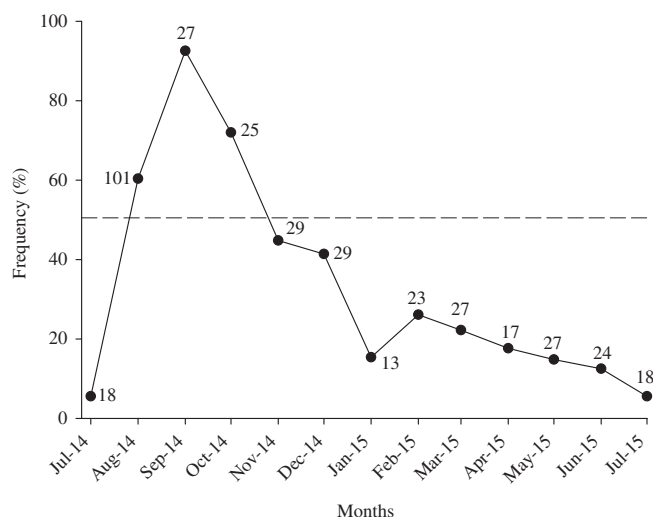
FIG. 2. A 1-year cycle showing the monthly frequency of an opaque growing edge in sagittal otoliths of *Meuschenia scaber*, from July 2014 to July 2015. ●, Monthly frequency with sample size; ----- of 50% of otoliths with an opaque edge.

signs of slow growth (60–93%) (Fig. 2). These results indicate that one opaque and one translucent zone is deposited each year. Because the opaque zone is deposited during the spawning season (Visconti *et al.,* 2017), it was chosen for annual age determination.

AGE ESTIMATION AND PRECISION OF READING

Juvenile *M. scaber* (62–108 mm L_T) collected in February 2015 and January 2016 ranged from 86 to 153 days (Table I) and displayed a strong linear relationship between otolith mass and age ($r^2 = 0.94$). The position of the maximum count for each otolith showed that the first annual growth check was unlikely to be hidden within the core [Fig. 1(b)].

The decimal age was estimated from sagittal otoliths of 295 female and 356 male *M. scaber*; 98·5% of these were <11 years old (0+ to 10 years). Maximum ages for females and males were 17·1 and 9·8 years, respectively. The average percentage error ($\overline{E}$%) between first and second counts was 4·26 ± 0·38 S.E. and the mean C.V. was 5·7% ± 0·5 S.E.

GROWTH PARAMETERS

The rVBGF (Francis, 1988) was used to describe growth in length of female and male *M. scaber* and the resulting parameters are given in Table II. The growth trajectories of males and females overlapped, suggesting little difference in growth pattern between sexes in this species, although males grew slightly faster initially than females [Fig. 3(a)]. Despite a lack of difference between the growth trajectories of the two sexes, likelihood-ratio tests revealed significant differences between females and males in the fitted rVBGF growth curves ($P < 0.001$) (Table III). As a result, growth in females and males was best described by two different curves (null hypothesis on a

TABLE I. Back-calculated estimate of date of birth (DOB) based on juvenile otoliths ($n = 17$) of *Meuschenia scaber* collected in March 2015 and February 2016 in the Hauraki Gulf

Fish	Date of catch	Depth (m)	Time (hours)	L_T (mm)	M_O (mg)	Sex	Age (days)	DOB
1	2 March 2015	3–5	2130	91	0·2622	F	143	10 October 2014
2	2 March 2015	3–5	2130	105	0·2781	F	153	30 September 2014
3	2 March 2015	3–5	2130	93	0·2473	F	132	21 October 2014
4	2 March 2015	3–5	2130	105	0·2756	F	148	5 October 2014
5	2 March 2015	3–5	2130	103	0·2683	M	137	16 October 2014
6	2 March 2015	3–5	2130	104	0·2555	F	136	17 October 2014
7	2 March 2015	3–5	2130	102	0·2706	M	136	17 October 2014
8	2 March 2015	3–5	2130	90	0·231	M	122	31 October 2014
9	2 March 2015	3–5	2130	82	0·1933	F	91	1 December 2014
10	2 March 2015	3–5	2130	101	0·2816	F	138	15 October 2014
11	2 March 2015	3–5	2130	108	0·2918	M	150	3 October 2014
12	2 February 2016	3	1130	62	0·1954	F	91	3 November 2015
13	2 February 2016	3	1130	74	0·2127	M	105	20 October 2015
14	2 February 2016	3	1130	75	0·196	F	86	8 November 2015
15	11 February 2016	3	1030	74	0·2165	F	104	30 October 2015
16	11 February 2016	3	1030	77	0·2232	M	109	25 October 2015
17	11 February 2016	3	1030	99	0·2533	F	128	6 October 2015

L_T, Total length; M_O, otolith mass.

coincident curve for males and females was rejected) and suggested a significant difference between the sexes in mean size at ages 1, 3 and 5 years. As female and male growth trajectories appeared similar however (with the exception of maximum age), a combined growth curve is also provided [Fig. 3(a)].

Differences between the sexes in growth patterns were comparatively more evident in terms of mass. Growth in mass was initially faster in males, but slowed more quickly than in females on attaining maturity, resulting in a lower asymptotic mass for males [Fig. 3(b)]. The difference between the fitted growth curves for the two sexes was significant ($P < 0.001$), as were differences between the parameters M_∞ ($P < 0.001$) and K ($P < 0.01$).

TABLE II. Sex-specific growth of *Meuschenia scaber* from the Hauraki Gulf, showing best-fit reparameterized (rVBGF) and standard von Bertalanffy (VBGF) growth-function parameters

Sex	n	rVBGF			VBGF				
		L_1 (mm)	L_3 (mm)	L_5 (mm)	L_∞ (mm)	K (year^{-1})	t_0 (years)	$-\lambda$	σ (mm)
F	295	178·7	264·2	275·8	279·7	0·74	−0·24	1102·2	18·24
M	356	196·8	272·3	279·4	282·2	0·9	−0·1	1420·9	17·94
Combined	651	188·6	268·9	277·9	279·1	0·47	−0·03	2537	18·5

n, Sample size; L_1, mean size at age one; L_3, age three; L_5, 5 years; L_∞, mean asymptotic length, K, curvature parameter; t_0, theoretical age at size zero; $-\lambda$, negative log-likelihood; σ, S.D.
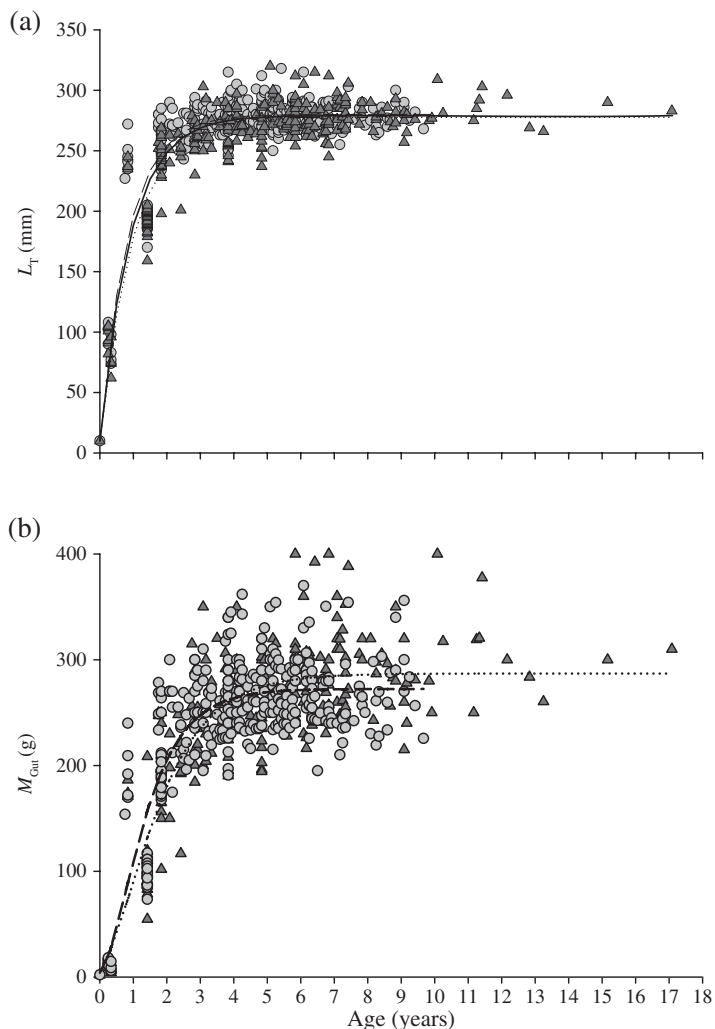
FIG. 3. (a) Reparameterized von Bertalanffy growth function (rVBGF) curve showing total length (L_T)-at-age fitting for *Meuschenia scaber* in the Hauraki Gulf, New Zealand and (b) the best fit gutted mass (M_{Gut})at age von Bertalanffy growth curves. ——, Best-fit function for combined sexes; ·········· and ▲, female growth curve; ------ and ●, male growth curves.

LENGTH–MASS RELATIONSHIP AND CONDITION

The relationship between total length (L_T) and total mass (M_T) was $M_T = 0.000018L_T^{2.988456}$ ($r^2 = 0.99$, $n = 295$) for females, $M_T = 0.000030L_T^{2.988981}$ ($r^2 = 0.98$, $n = 364$) for males and $M_T = 0.000027L_T^{2.903492}$ ($r^2 = 0.97$, $n = 659$) combined (Fig. 4). The 95% C.I. of the parameter b (slope) ranged between 2·95 and 3·03 for females and 2·80 and 2·95 for males. The ANCOVA revealed significant difference in the slope ($F_{2,649} = 9999.231$, $P < 0.001$) and intercept ($F_{2,649} = 6635.130$, $P < 0.001$) between sexes. The mean monthly relative condition (K_{nj}) ranged from 1·09 (July 2014) to 0·97 (December 2014) in females and 1·10 (November 2014) and

TABLE III. Sex-specific growth of *Meuschenia scaber* from the Hauraki Gulf showing results of likelihood ratio (LR) test comparing growth between males and females at mean size at age one (L_1), three (L_3) and five (L_5) years respectively.

Hypothesis	n	$-\lambda$	LR	d.f.	P
Base	6	2530·83	–	–	–
Coincident curves	3	2544·69	79·66	3	<0·001
L_1	5	2540·53	56·03	1	<0·001
L_3	5	2545·69	86·98	1	<0·001
L_5	5	2532·91	12	1	<0·001

$-\lambda$, Reparameterized von Bertalnffy growth negative log-likelihood function.
Coincident curves represent the null hypothesis of no difference in growth between the sexes, and base case the alternative hypothesis of sex-specific growth trajectories.

0·96 (July 2015) in males (Fig. 5). Female condition was highest in July, declining in August, when relative ovary mass increased (Visconti *et al.,* 2017) and showed a slight peak in January and February, immediately following the spawning season. Male condition also declined with the onset of spawning, but then increased again in the middle of the 5 month spawning season, to produce a peak that continued through to mid-summer, once spawning was over.

AGE AT MATURITY

The age at maturity (T_{50}) of female *M. scaber* was 1·53 (95% C.I. 1·09−1·69) and 1·52 (95% C.I. 1·15−1·67) for males (Fig. 6). The T_{95} was 1·69 (95% C.I. 1·42−2·11) and 1·63 (95% C.I. 1·43−2·12) for females and males, respectively. A likelihood ratio
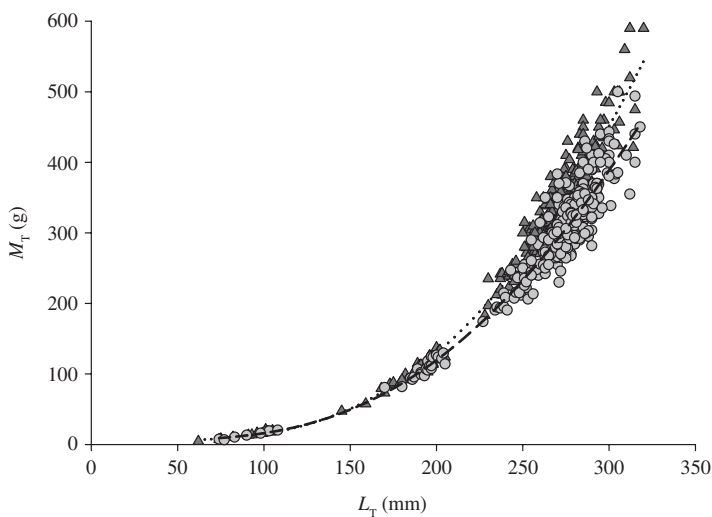

FIG. 4. Total length (L_T)−mass (M_T) relationship for *Meuschenia scaber* ___ and ▲, females; .... and ◎, males.
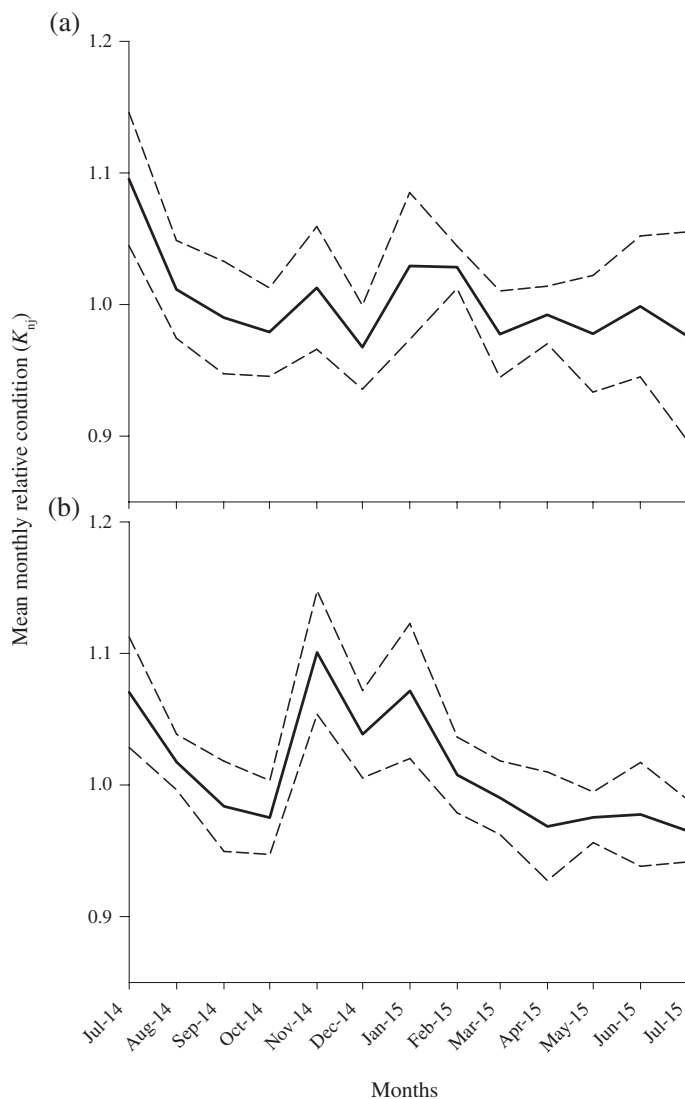
(a)

(b)

FIG. 5. Relative condition factor (K_{nj}) of (a) female and (b) male *Meuschenia scaber* from July 2014 to July 2015. ------, 95% C.I.

test showed no significant difference between the logistic maturity ogives for each sex ($P > 0.01$).

MORTALITY

The instantaneous total mortality (Z) estimates based on the catch-curve regressions for females and males were 0·37 ($r^2 = 0.85$) and 0·75 ($r^2 = 0.87$), respectively. The mortality estimates based on the CR method were 0·51 for females and 0·63 for males.
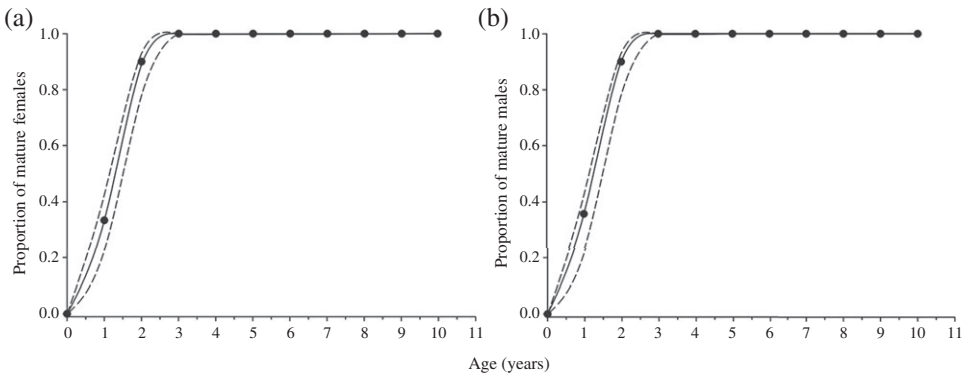
FIG. 6. Age at maturity (T_{50}) frequency distribution (●) of mature active (a) female ($T_{50} = 1\cdot53$ years) and (b) male ($T_{50} = 1\cdot52$ years) *Meuschenia scaber* in the Hauraki Gulf during the spawning season. ------, 95% C.I.

DISCUSSION

The present study validated the suitability of sagittal otoliths for ageing purposes in monacanthids and revealed essential life-history traits of *M. scaber*. It appears to be a fast-growing species with a maximum age of at least 17 years and with most individuals reaching sexual maturity at 1–2 years of age.

The otolith-based ageing protocol for *M. scaber* juveniles proved suitable for this species and generated ages between 86 and 153 days. There was however, some limitation on reading daily increments: it was increasingly difficult to distinguish daily rings due to inconsistency in the alternation of opaque and translucent zones after 153 days. The alternation of opaque and translucent zone appearance in early life-stage fish has been documented to be affected by behaviour (including vertical movements) and physiology of fish species (Pannella, 1971; Milicich & Choat, 1992; Fowler, 1995). Juveniles of *M. scaber* on reefs in the Hauraki Gulf are known to rapidly change their time in the pelagic environment and growth rates before settling at between 22 and 66 days of life (Kingsford & Choat, 1985; Kingsford & Milicich, 1987) and this could explain the irregularity of ring deposition at this stage. In addition, the limitation could also be related to the method adopted in this study. Furthermore, present results could be considered additional to those reported by Kingsford & Milicich (1987) where age estimation was based on whole otoliths and individuals were aged to 66 days.

The ETA revealed that opaque zone formation in *M. scaber* otoliths had a clear annual cycle; suggesting one opaque and one translucent zone is deposited each year. The opaque zone is laid down between August and October (austral spring), with peak proportion of opaque otolith margins coinciding with the peak of gonad maturation (spawning season) recorded for *M. scaber* by Visconti *et al*. (2017). On the other hand, the minimum seasonal temperature recorded for the Hauraki Gulf during the same period (Paul, 1968) may represent the trigger for opaque zone deposition, as has been suggested for other species (Loubens, 1978; Ralston & Williams, 1989; Newman *et al.,* 1996). Overall, the timing and periodicity of opaque zone deposition described here is also consistent with that displayed in a number of temperate and southern-hemisphere fish species (Beckman & Wilson, 1995; Trip *et al.,* 2011*a*).

The analysis of annual increments in *M. scaber* otoliths revealed maximum ages of at least 17·1 and 9·8 years for females and males, respectively. The $\overline{E}\%$ and C.V. values between readings were below those reported as cut off by Campana (2001) for other ageing studies based on otoliths and confirm an appropriate level of reading precision for this study. Miller *et al*. (2010) reviewed reported longevity for species of the family Monacanthidae and found a maximum recorded age of 9 years, attained by both *N. ayraud* and *Thamnaconus septentrionalis* (Günther 1874). Although the maximum age of *M. scaber* males recorded in this study is consistent with the lifespan reported for other monacanthids, females are clearly longer lived. Such a difference in longevity between sexes has been also described by Barrett 1995 for *P. vittiger* in temperate Tasmanian waters, where males reached 3·5 years and females 5+ years. In addition, tropical fish species are known to have a shorter lifespan in comparison with temperate water counterparts (Choat & Robertson, 2002). This also appears to be the case in *M. scaber*, where, at 17 years, females achieve the greatest longevity reported for monacanthids so far, with males living up to 10 years. Tropical and subtropical monacanthid genera such as *Stephanolepis* (Gill 1871) and *Monacanthus* (Oken 1817) only live up to 3 and 5 years, respectively, although this could reflect the phylogenetic distance between the genera (Santini *et al.,* 2013).

Meuschenia scaber displayed very fast growth in the first 2 years of life in both sexes. In general, a pattern of early fast growth in fishes could be associated with a reduced longevity (Metcalfe & Monaghan, 2003) and is thought to reflect predator response (*i.e.* larger body size reduces the risk of predation), trade-offs between longevity and reproductive success and competition between males for access to females (Roff, 1992). *Meuschenia scaber* juveniles rely on the *E. radiata* kelp-forest habitat where food availability is high (*i.e.* supports a pattern of fast growth) and some protection is offered against predators (Choat & Ayling, 1987; Anderson & Millar, 2004). They have an early age at maturity ($T_{50-95} = 1-2$ years) that may reflect trade-offs between longevity and reproductive success. Furthermore, there was little difference between the sexes in growth pattern, although males grew slightly faster than females in mass. Despite there being a statistical difference between the female and male growth trajectories in both length and mass, those differences were not clearly apparent on the growth curves, suggesting that these differences may not be biologically significant. Overall, the growth rates of both sexes declined immediately following attainment of reproductive maturity ($T_{95} = 2$ years) and consequently females and males both achieved an early asymptotic length (L_∞). In addition, since samples of *M. scaber* were selected randomly with regard to length within each sex, the age structure presented here is likely to reflect the population in the area sampled. The shallow reef habitat sampled in this study is not subject to trawling and consequently the age structure observed for males and females is unlikely to be a function of fishery selectivity.

Males and females did not differ in either size at maturity (Visconti *et al.,* 2017) or age at maturity (present study). In addition, the shorter longevity of males is reflected by higher rates of total mortality ($Z = 0\cdot75$) in comparison with that of females ($Z = 0\cdot37$). Higher mortality in males is probably a consequence of having to defend territories during the five-month spawning season, as has been documented in other fish species (Metcalfe & Monaghan, 2003) as a result of either high energy demands (Roff, 1992) or increased vulnerability to predation. Slower growth in mass after maturity (below) suggests that the energy demands of spawning are greater for males.

The length–mass relationships in *M. scaber* showed different patterns between the sexes, with females showing isometric growth ($2 \cdot 99 \pm 0 \cdot 02$) and males negative allometric growth ($2 \cdot 87 \pm 0 \cdot 015$). Both the slope *b* and the intercept *a* values differed significantly between sexes, supporting the hypothesis that females attain heavier mass at length, allowing them to carry large ovaries, with higher batch fecundity. This result is also consistent with two other findings: the greater body depth of females recorded by Visconti *et al.* (2017); the difference in the mass at age between sexes (present study). Thus, the mass-at-age VBGF model showed an initial fast growth for males that was maintained until the sexual maturity at which females displayed a faster somatic growth. These trends indicate that males might invest more available energy into reproduction (*e.g.* digging nests, defending territories and attracting the partner) than females that might feed between spawning events.

Female condition was highest in July (austral winter), declining in August, when relative ovary mass increased (Visconti *et al.,* 2017) and showed a slight peak in January and February (austral summer), immediately following the spawning season. Male condition also declined with the onset of spawning, but then increased again in the middle of the 5-month spawning season, to produce a substantial peak that continued through to mid-summer, 2 months after spawning ceased. The highest proportion of otoliths with opaque margins was recorded in August–October, which coincides with the decline in condition associated with the onset of maturity; suggesting the deposition of opaque material in sagittal otoliths in *M. scaber* might be the result of a trade-off between the nutritional resources required for reproduction (*i.e.* gonad development, courting) and growth (Rochet, 2000).

In conclusion, this research describes the life-history traits of a common monacanthid species in Australasian waters, *M. scaber*. The life-history parameter estimates presented here indicate small differences between the sexes in growth, but substantial differences in lifespan and mortality, as seen in other species of the same family (Miller *et al.,* 2010). More importantly, *M. scaber* is the longest-living monachantid species described so far and possibly the oldest documented for the entire suborder. Although this represents the first comprehensive age-based study for *M. scaber*, more work is needed to examine the magnitude of demographic variation among populations in response to environmental variation. Despite the perception that ageing monacanthids is problematical due to difficulties in handling such fragile, small and unusually shaped otoliths and detecting the periodicity of ring deposition, this study provides a clear example of how otoliths of fishes from high-latitude reef systems are suitable for age-based demography studies.

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