

Length- and age-based demographics of exploited populations of stout whiting, *Sillago robusta* Stead, 1908

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Summary

This study assessed variability in the length and age compositions, longevity, length-at-age and rates of growth and mortality of the east Australian stout whiting *Sillago robusta* Stead, 1908 population harvested by demersal trawl fisheries. Sampling was done over 2 years and was spatially stratified across three depth strata between 11 and 90 m at two locations approximately 400 km apart. There were no consistent depth-related differences in length and age compositions, but the mean and median length and age of the population was greater at the lower latitude location. Age classes 2 and 3 years dominated samples in the north, and 1 and 2 years in the south. Observed longevity was 10 years in the north, and 6 years in the south. Mean length-at-age was not consistently different between sexes, years or locations, nor did the von Bertalanffy growth function differ significantly between sexes, even though females had a greater estimated L_{∞} (23.45 cm FL) compared to males (22.36 cm FL). Estimated natural mortality (M) ranged between 0.42 and 0.77, using age- and length-based methods. Age-based catch-curve analyses identified the instantaneous rate of total mortality (Z) to range between 1.48 and 2.70, with subsequent estimates of fishing mortality (F) ranging between 1.15 and 2.00, being greater than M . Exploitation rates (E) were greater than 0.7, indicating that *S. robusta* at the study locations was heavily fished. The data provided here can be used as a basis to evaluate future fishery- and climate-related changes in the population demographics of east Australian *S. robusta*.

1 | INTRODUCTION

Length- and age-based data provide vital insights into the demographic and life history dynamics of wild teleost population, forming the basis of many fisheries assessment models (Campana, 2001; Hilborn & Walters, 1992; Lai, Gallucci, Gunderson, & Donnelly, 1996). In particular, knowledge of temporal and spatial shifts in rates of growth, longevity and mortality schedules of populations can help determine population changes associated with anthropogenic (e.g. fishing) and environmental (e.g. changing climate) perturbations (Patterson et al., 2001; Ricker, 1975). Reports of temporal changes in population levels and demographics of harvested teleost species abound, particularly

those subject to large trawl fisheries (Fogarty & Murawski, 1998; Rijnsdorp, van Leeuwen, Daan, & Heesen, 1996). It is imperative that exploited fish populations be monitored and assessed with regularity so that management strategies are modified accordingly (Walters & Martell, 2004).

Many of the 31 species of the teleost family Sillaginidae are exploited in commercial, recreational and artisanal fisheries (Gray & Kennelly, 2003; Henry & Lyle, 2003; McKay, 1992), with several subject to substantial demersal trawl-based fisheries (Graham, Broadhurst, & Millar, 2009; McKay, 1992; Panhwar, Liu, Khan, & Siddiqui, 2012). Important age, growth and longevity data are available for several harvested species, including the oriental whiting *Sillago aeolus* Jordan

& Evermann, 1902 (Rahman & Tachihara, 2005), Japanese whiting *S. japonica* Temminck & Schlegel, 1843 (Yokota, Kitada, & Watanabe, 1999), silver whiting *S. sihama* (Forsskål, 1775) (Reddy & Neelakantan, 1992), yellowfin whiting *S. schomburgkii* Peters, 1865 (Hyndes & Potter, 1997), school whiting *S. bassensis* Cuvier, 1829 (Hyndes & Potter, 1996), trawl whiting *S. flindersi* McKay, 1985 (Gray, Barnes, Ochwada-Doyle et al., 2014), trumpeter whiting *S. maculata* Quoy & Gaimard, 1824 (Kendall & Gray, 2009), sand whiting *S. ciliata* Cuvier, 1829 (Ochwada-Doyle, Stocks, Barnes, & Gray, 2014), and spotted whiting *Sillaginodes punctata* (Cuvier, 1829) (Fowler, McLeay, & Short, 2000; Hyndes, Platell, Potter, & Lenanton, 1998). These studies show that, in general, sillaginids grow quickly, have longevities between 4 and 14 years, and have populations dominated by a few young age-classes (Kendall & Gray, 2009). Even with comparatively short-lived species, it is imperative that age determination and longevity estimates are accurate, as they are fundamental to fisheries assessments; under- or over-estimation of either can have crucial consequences for management decisions (Campana, 2001; Newman, Cappo, & Williams, 2000).

The stout whiting *Sillago robusta* Stead, 1908 is endemic to Australia but consists of two disparate populations extending between approximately 24 and 34°S on the west and east coasts (Gray, Barnes, van der Meulen et al., 2014; McKay, 1992). The species has an inshore coastal distribution and is primarily associated with soft sediments <100 m depth (McKay, 1992). On the east coast, the species forms part of a limited-entry quota-managed trawl fishery in the northern sector (Queensland) and a non-quota multi-species trawl fishery in the southern sector (New South Wales; NSW). Total reported east coast landings have fluctuated between 800 and 1,500 tonnes per annum over the past 10 years, but have been less than 900 tonnes since 2011 (Flood et al., 2014). Life history information, including growth and reproductive characteristics, are known for western (Hyndes & Potter, 1996) and eastern (Butcher & Hagedoorn, 2003; Gray, Barnes, van der Meulen et al., 2014) populations. However, the age-based information for the species on both coasts is founded on interpretation of whole otoliths, which can be problematic if not validated correctly and can lead to underestimating the true ages of older individuals (Campana, 2001). Moreover, for eastern populations the data are limited to those occurring in the northern range of their distribution and the applicability of results across the species eastern distribution is not known.

Numerous teleost species display plasticity in demographic characteristics across a range of spatial scales (Gust, Choat, & Ackerman, 2002; Williams, Davies, Mapstone, & Russ, 2003). For example, the length and age compositions of species can vary across depths, and latitudinal clines in growth and longevity are common (Caselle et al., 2011; Ruttenberg, Haupt, Chiriboga, & Warner, 2005; Sala-Bozano & Mariani, 2011; Stocks, Gray, & Taylor, 2014). Given the sustained exploitation of *S. robusta* on the east Australian coast, a region experiencing heightened climate-related oceanographic and environmental change (Lough & Hobday, 2011), there is a need for a greater understanding of spatial variability in the demographic characteristics of *S. robusta* for incorporation in future management deliberations. This study specifically investigated variability in length-at-age, growth,

longevity, age compositions and mortality schedules of east Australian *S. robusta*, as well as provided validation of an otolith-based ageing protocol.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling procedures

Samples of *S. robusta* were collected from 3 depth ranges: 11–30 m, 31–60 m and 61–90 m (hereafter termed shallow, mid- and deep depths, respectively), over inner continental shelf waters adjacent to Yamba (29°26'S, 153°20'E), and Newcastle (32°55'S, 151°45'E) off eastern Australia. A chartered ocean prawn-trawl vessel from each port made two replicate 60 min tows in each depth strata at night, every 4 weeks (within 1 week of the new moon), between November 2005 and November 2007 at Yamba, and between October 2006 and November 2007 at Newcastle (see Gray, Barnes, van der Meulen et al., 2014 for greater operational details).

The total number and weight of *S. robusta* captured in each replicate tow (sample) was determined onboard the vessel; either the whole catch, or a random sub-sample of the catch from each tow, was measured for fork length (FL, nearest 1 mm) for length composition analyses. A subsample of 60 individuals (when caught) from each depth was retained for processing in the laboratory to be measured for FL, weighed (0.1 g), sexed and with their sagittal otoliths removed for age analyses.

2.2 | Age estimation and validation

Sectioned sagittal otoliths were used to estimate the age of *S. robusta*. Otoliths were embedded in blocks of clear cast polyester resin and three to four transverse sections (approx. 0.7 mm) were cut through the otolith core using a diamond saw. The resulting sections were mounted on a microscope slide, polished until the banding on sections became clear, then viewed with a compound microscope fitted with a digital camera using reflected light against a black background. The section cut closest to the otolith core was used for reading. Otolith sections displayed a pattern of narrow opaque (light) and broad translucent (dark) zones and assignment of age was based on counts of completed opaque zones from the focus to the outer edge along the line of the sulcus. Each opaque zone was marked and the distance between successive opaque zones was measured using Image J software, after which digital images of each section were recorded. All measurements were made along the dorsal edge of the sulcus to the nearest 0.05 mm. Due to the species extended spawning strategy (Gray, Barnes, van der Meulen et al., 2014), there was no adjustment of counts of opaque zones based on month of capture, but counts were adjusted (+1) for individuals where the first opaque growth zone was obscured in the core growth. Sections were interpreted without the knowledge of the length or sex of the fish, or the date and location of capture; all sections were read twice without the knowledge of the first interpretation. In cases where the two readings differed, the sections were examined a third time, to assign a final age.

Marginal increment (MI) analysis was used to determine the periodicity of formation of opaque zones. The MI was expressed as: (i) for fish with one opaque zone, the distance from the first opaque zone to the otolith edge as a proportion of the distance from the focus to the first opaque zone, and (ii) for fish with two or more opaque zones, the distance from the most recently completed opaque zone to the otolith edge as a proportion of the last completed increment. Mean MI (± 1 SE) was calculated for each separate age group and for all ages combined for each month. Otolith edges were also examined and ascribed a value of 'opaque' or 'translucent'.

2.3 | Length-at-age and growth

Differences in the mean FL-at-age of *S. robusta* were tested using 3 factor permutational analyses of variance (Anderson, 2001). The first analysis tested for differences between years, sexes and age classes (2–8) was for samples collected at Yamba; the second analysis tested for differences between locations (Yamba vs. Newcastle), sexes and age classes (1–4). In both analyses, the model considered all factors fixed, and Type III (partial) sums-of-squares were calculated using 9,999 unrestricted permutations of the data.

The von Bertalanffy growth function (VBGF) was fitted to the FL-at-age data separately for each sex and location (combined across years for Yamba). Differences in growth between sexes (but not locations; see results) were tested by comparing the VBGF fitted across equal age classes (ages 2–8) using the analysis of residual sums of squares (ARSS) method (Chen, Jackson, & Harvey, 1992).

2.4 | Length and age compositions

Annual length-frequency histograms of *S. robusta* from each depth and for all depths combined (weighted by monthly catch) were generated for both locations. The corresponding age compositions of populations were calculated by applying separate age-length keys for each location to the relevant length-frequency data. Kolmogorov-Smirnov (KS) tests were used to determine whether the length and age compositions differed among depths at each location.

2.5 | Mortality and exploitation

Estimates of the instantaneous rate of total mortality (Z) were made for each depth and year separately, and for all depths combined, at Yamba and Newcastle, using the age-based catch curve method (Ricker, 1975). The natural logarithm of the proportion of fish in each age class (N_t) was plotted against their corresponding age class (t) and a linear regression was fitted to data to the right of the highest value with Z determined as the slope of the descending regression. For each analysis, we assumed that the most abundant age class in each sample (3 years for Yamba, 2 years for Newcastle) was fully recruited to the sampled population. Standard error (SE) and r^2 values were calculated for each regression. These analyses assumed that the selectivity, recruitment and growth of fish were constant across years.

The instantaneous rate of natural mortality (M) was estimated using three age-based methods: (i) $\ln M = 1.46 - 1.01 \ln(tm)$ (Hoenig, 1983); (ii) $M = 4.22/tm$ (Hewitt & Hoenig, 2005); (iii) $M = -\ln(0.01)/tm$ (Quinn & Deriso, 1999), where tm is the maximum age in years. Also one length-based method: $M = -0.0152 - 0.2790 \ln(L_\infty) + 0.6545 \ln(k) + 0.4634 \ln(T)$ (Pauly, 1980), where L_∞ and k are the von Bertalanffy growth coefficients, and T is water temperature ($^{\circ}\text{C}$). We used an average annual water temperature of 21°C for Yamba and 20°C for Newcastle (Ives, Scandol, Montgomery, & Suthers, 2009). The Hoenig (1983) method was based on the assumption that 1% of individuals reach the maximum attainable age.

Fishing mortality (F) was estimated by subtracting the highest and lowest estimates of M (of the four methods employed) from the corresponding estimates of Z , which also provided two estimates of exploitation rate (E): $E = F/Z$.

3 | RESULTS

A total of 2,138 sectioned otoliths were examined. This included 649 female, 843 male and 182 juveniles at Yamba and 235 female, 178 male and 51 juveniles at Newcastle.

3.1 | Ageing: Periodicity of opaque zone formation

The greatest proportion of otoliths with opaque edges occurred in September (23.1%), after which proportions decreased by January (2.4%), remained relatively low until May, then increased (Figure 1a). The MI displayed a cyclical pattern, with the I_M being greatest in August (0.45) then decreasing until February (0.31), after which it again increased (Figure 1b). Both analyses indicated that the opaque growth zone was deposited once per annum, between September and January.

3.2 | Longevity, length-at-age and growth

Differences in longevity were evident between locations: oldest female and male were 8^+ (21.5 cm FL) and 10^+ (22.2 cm FL) years, respectively, at Yamba, compared to 6^+ (21.8 cm FL) and 4^+ (20.5 cm FL) years, respectively, at Newcastle. The largest individual sampled was 23.7 cm FL (6^+ years, female) at Yamba.

There was considerable variation in length-at-age among individual *S. robusta* of both sexes (Figure 2). Subsequently, the mean FL-at-age did not differ significantly between sexes or locations, but did differ significantly among age classes (Table 1), with the mean FL increasing with each age category (Figure 2). For the significant interaction terms (Year \times Age, and Location \times Age), the pairwise comparisons identified that mean FL-at-age of *S. robusta* aged 3 years was significantly greater in 2007 than 2006 at Yamba, and at Newcastle than at Yamba. The pairwise comparisons did not detect any other significant differences in other age categories.

The VBGF did not differ significantly between males and females at Yamba (ARSS test: $F = 1.715$; $df = 3, 1,820$; $p = .162$). This occurred even though the VBGF parameters differed between sexes (female:

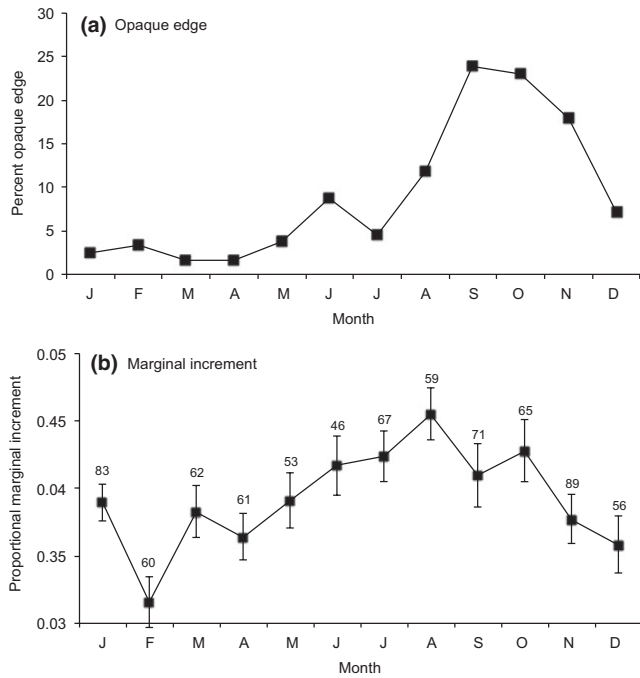


FIGURE 1 Age validation of *Sillago robusta*. (a) Total percentage of sectioned otoliths that had opaque edges each month for data pooled across the study period of November 2005 to November 2007. (b) The mean (± 1 SE) marginal increment (MI) for all ages combined each calendar month pooled across 2005–2007. *n*, sample size for each month; SE, standard error

$L_{\infty} = 23.45$ cm FL, $k = 0.31$, and $t_0 = -0.44$; male: $L_{\infty} = 22.36$ cm FL, $k = 0.34$, and $t_0 = -0.31$; Figure 2). No sensible growth curve could be generated for either sex at Newcastle due to the lack of older individuals (>4 years) in the samples.

3.3 | Length and age compositions

Sillago robusta between 5 and 23 cm FL were present in samples, but fish between 10 and 18 cm FL were most predominant across all depths (Figure 3). At both locations and for each year, the length and age compositions of samples differed significantly among depths (multiple SNK tests, $p < .05$ in all cases). The mean FL and age of sampled fish was greater at Yamba than at Newcastle. Individuals of 2 and 3 years contributed the most to the age composition of samples across all depths at Yamba, whereas 2-year old-fish dominated the shallow strata and 1-year-olds the deep strata at Newcastle (Figure 3). Few fish greater than 5 years were present in samples from any depth strata. When length and age data for each location were pooled across depths, fish aged two and three dominated the population at Yamba, and 2-year-olds at Newcastle (Figure 4).

3.4 | Mortality and exploitation

Estimates of *Z* ranged between 1.49 and 2.11 for individual depths at Yamba, being 1.61 in 2006 and 1.72 in 2007 at Yamba, and 2.70 at Newcastle for samples pooled across all depths (Table 2). The

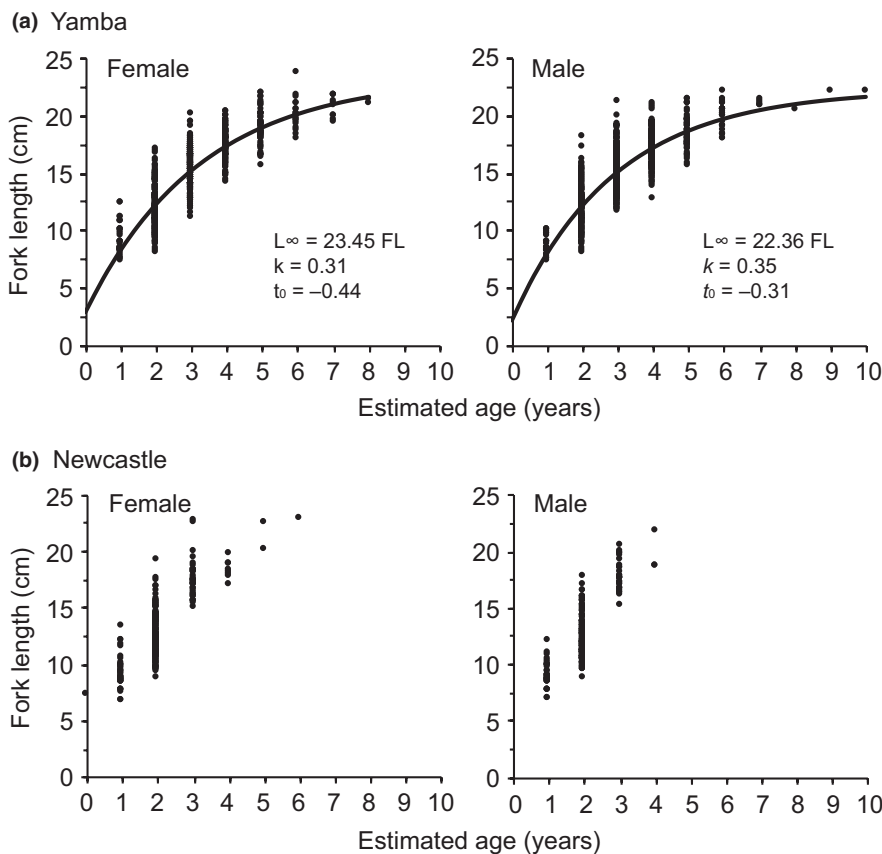


FIGURE 2 Growth and length-at-age of *Sillago robusta*. (a) von Bertalanffy growth curves and fork length-at-age data of female and male *S. robusta* captured across the three sampled depth ranges (11–90 m) over the inner continental shelf waters at Yamba (29°26'S, 153°20'E) during the study period of November 2005 to November 2007. (b) Fork length-at-age data of female and male *S. robusta* captured across the three sampled depth ranges (11–90 m) over the inner continental shelf waters at Newcastle (32°55'S, 151°45'E) during the study period of October 2006 to November 2007

TABLE 1 Summary of Permutational Analyses of Variance (Permanova) (Anderson, 2001) testing for differences in fork length (FL)-at-age of *Sillago robusta*. (a) Test of differences in FL-at-age of *S. robusta* between years (2006 and 2007), sex (male vs. female) and age (classes 2–8) captured across the three sampled depth ranges (11–90 m) over the inner continental shelf waters at Yamba (29°26'S, 153°20'E). (b) Test of differences between locations (Yamba – 29°26'S, 153°20'E and Newcastle – 32°55'S, 151°45'E), sex (male vs. female) and age classes 1–4, captured across the three sampled depth ranges (11–90 m) over the inner continental shelf waters

Factor	df	MS	Pseudo-F	P (perm)
(a) Comparison between years, and sex at Yamba				
Year (Y)	1	2.25	1.08	ns
Sex (S)	1	0.41	0.20	ns
Age (A)	6	689.08	331.86	***
Y × S	1	1.49	0.72	ns
Y × A	6	6.52	3.14	**
S × A	6	0.95	0.46	ns
Y × S × A	6	2.07	1.00	ns
Residual	1,444	2.08		
(b) Comparison between Yamba and Newcastle, and sex				
Location (L)	1	0.45	0.20	ns
Sex (S)	1	0.15	0.07	ns
Age (A)	3	849.09	377.03	***
L × S	1	4.70	2.09	ns
L × A	3	66.57	29.56	***
S × A	3	1.30	0.58	ns
L × S × A	3	3.44	1.53	ns
Residual	1,677	2.25		

df, degrees of freedom; MS, mean square; Pseudo-F – pseudo f value; P (perm), significance of permutation test. ** $p < .01$, *** $p < .001$, ns $p > .05$.

corresponding rates of annual total mortality (A) ranged between 77% and 93% (Table 2). These estimates were based on inclusion of age classes 3–8 years for Yamba and 2–5 years for Newcastle.

Depending on the age-based estimation method, M ranged between 0.42 and 0.46 at Yamba and 0.70 to 0.77 at Newcastle (Table 2), using the observed maximum age of 10 years at Yamba and 6 years at Newcastle. The length-based estimate of M was 0.43 at Yamba, but no estimation could be made for Newcastle due to the lack of a sensible VBGF. All calculations of F were considerably $>M$, ranging between 1.15 and 1.30 at Yamba, and 1.93 and 2.00 at Newcastle (Table 2). The corresponding rates of E ranged between 0.71 and 0.76 across locations.

4 | DISCUSSION

4.1 | Age and growth

The MI analyses validated the use of counts of opaque zones on sectioned otoliths as annuli. This is concordant with reports for other Sillaginidae (Fowler & Short, 1998; Kendall & Gray, 2009; Rahman & Tachihara, 2005;

Yokota et al., 1999), and teleosts inhabiting temperate waters in general (Campana, 2001). The opaque zones on otoliths of *S. robusta* probably began to form during the late austral winter and early spring (August to September), but were not observed as being completed (i.e. counted) on some individuals until late summer (February). This spring-summer timing of completion of opaque zone formation concurs with that observed for western populations of *S. robusta* (Hyndes & Potter, 1996) and a range of other east Australian coastal and estuarine teleosts, including platycephalids (Barnes, Gray, & Williamson, 2011; Gray, Gale, Stringfellow, & Raines, 2002), scorpaenids (Stewart & Hughes, 2010), girellids (Gray, Ives, Macbeth, & Kendall, 2010; Stocks et al., 2014) and sparids (Gray, 2015; Hughes, Stewart, Kendall, & Gray, 2008).

The VBGF for *S. robusta* did not differ significantly between sexes, even though the observed maximum FL and estimated L_{∞} was greater for females than males. These data both coincide with, and contrast, previous reports of growth of *S. robusta*; Butcher and Hagedoorn (2003) reported no gender differences in growth ($L_{\infty} = 22.2$ cm FL), whereas Hyndes and Potter (1996) determined that males attained a slightly greater L_{∞} (17.2 cm FL) than females (16.9 cm FL). The largest *S. robusta* observed in the current study (23.7 cm FL) was similar to the 23.2 cm FL reported by Butcher and Hagedoorn (2003), both being greater than the 20.0 cm FL in the western population (Hyndes & Potter, 1996). These combined data suggest that *S. robusta* has flexible growth (and FL-at-age) characteristics within and between coastlines. Although such geographic differences could be attributed to a plethora of biotic and abiotic factors (Lappalainen, Tarkan, & Harrod, 2008; Stocks et al., 2014; Williams, Mapstone, & Davies, 2007), they further demonstrate within and among population levels of plasticity in growth characteristics of fish (Gust et al., 2002; Sarre & Potter, 2000), emphasizing the importance of regional demographic information of species for assessment purposes (Ruttenberg et al., 2005).

The estimated longevity of 10 years for *S. robusta* in the current study, which is in the upper range compared with other sillaginids (4–14 years; see Kendall & Gray, 2009), was greater than previous reports of 6 and 5 years for the western and northeastern population, respectively (Butcher & Hagedoorn, 2003; Hyndes & Potter, 1996). Such differences do not appear to be an artefact of the previous studies using whole otoliths to determine age; for the western populations the whole otolith readings were validated against sectioned otolith readings. Although it is probable that the older fish encountered in the current study were due to greater sampling intensity, we suggest that such differences may be partly attributable to the latitude of the study location. Latitudinal clines in length-at-age, growth and observed longevity are common among teleost species (Gray, 2015; Gray et al., 2010; Stocks et al., 2014).

The maximum ages of male and female *S. robusta* sampled at Yamba were nearly double those of *S. robusta* at Newcastle, which occur at a similar latitude to the study location of the western population (31–32°S). We suggest that because Newcastle is close to the southern distribution limit of the species, individual fish may survive only a few short years due to living at the extreme of their thermal tolerance limit (Lappalainen et al., 2008). Alternatively, early aged *S. robusta* could, as a life history strategy, migrate northwards to more tolerable conditions and to spawn. Several teleost (Gray & Barnes, 2015; Gray et al., 2012)

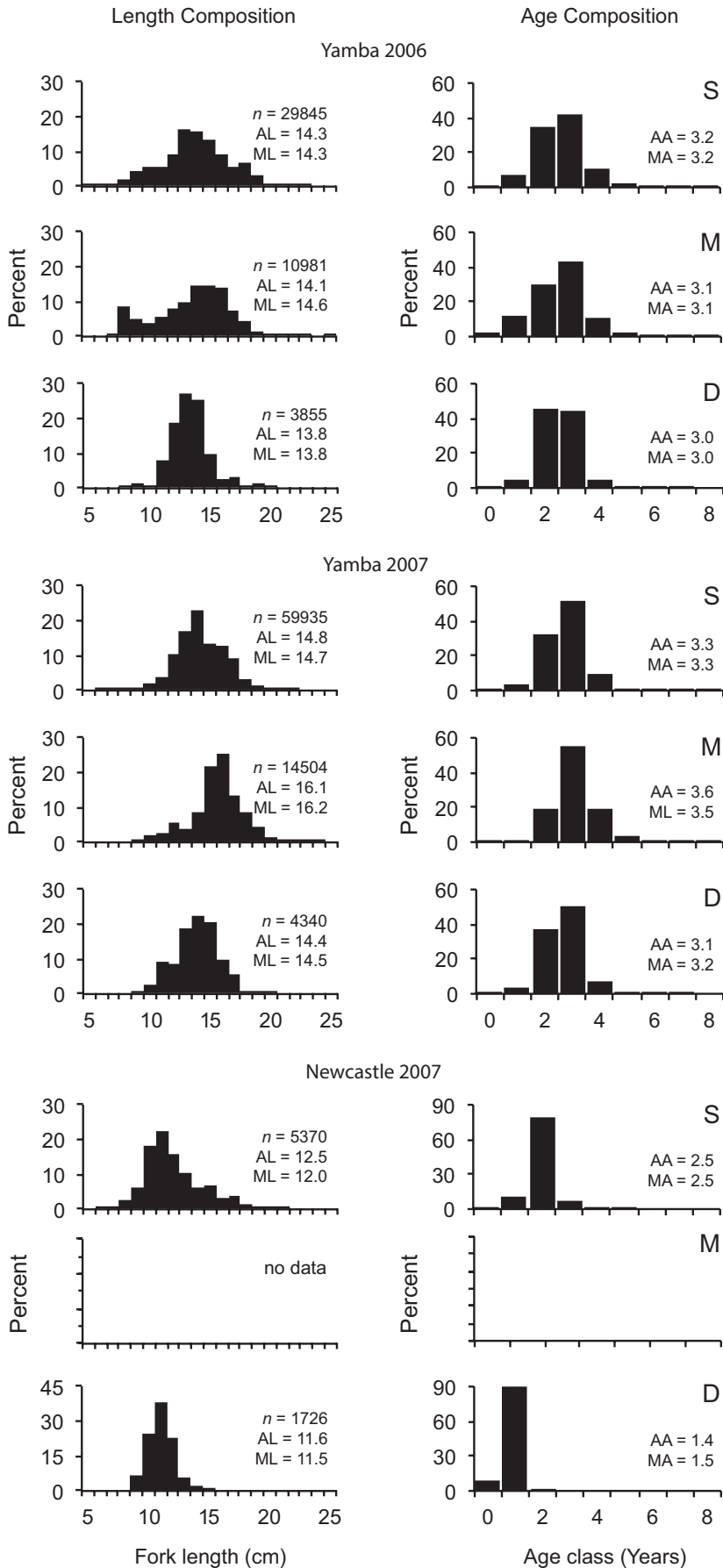


FIGURE 3 Fork length and age compositions of *Sillago robusta*. Fork length and age compositions of *S. robusta* for each depth strata (shallow: 11–30 m), mid (31–60 m), deep (61–90 m) over the inner continental shelf waters at Yamba (29°26'S, 153°20'E) during 2006 and 2007, and Newcastle (32°55'S, 151°45'E) during 2007. S, shallow strata (11–30 m); M, mid strata (31–60 m); D = deep strata (61–90 m). AL, average fork length FL (cm); ML, median fork length FL (cm); AA, average age (years); MA, median age (years); n, sample size

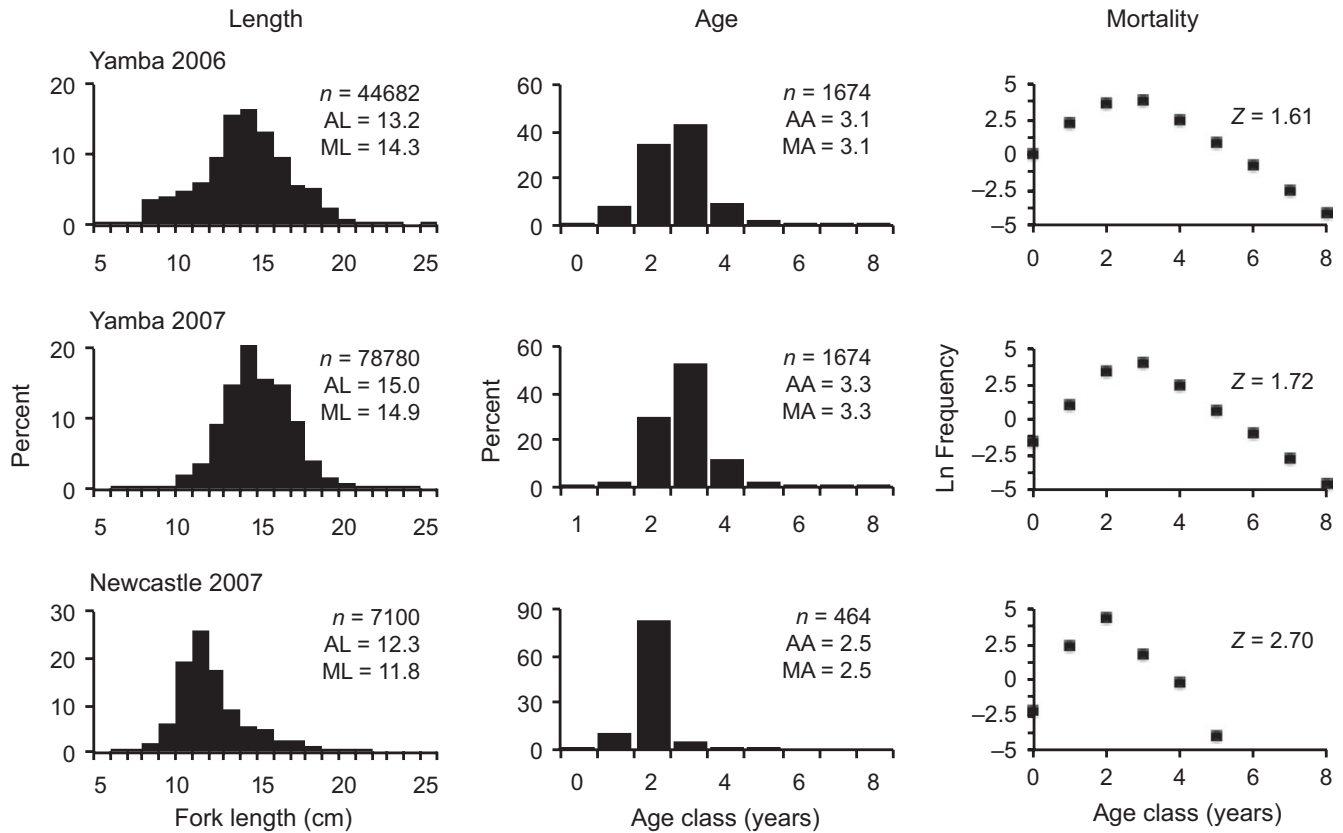


FIGURE 4 Fork length and age compositions and total mortality of *Sillago robusta*. Fork length and age compositions and catch curve analyses of *S. robusta* combined across three sampled depths (11–90 m) over the inner continental shelf waters at Yamba (29°26'S, 153°20'E) during 2006 and 2007, and at Newcastle (32°55'S, 151°45'E) during 2007. *n*, sample size; AL, average fork length FL (cm); ML, median fork length FL (cm); AA, average age (years); MA, median age (years); Z, total mortality

and invertebrate (Montgomery, 1990; Stewart & Kennelly, 1998) species migrate northward into the prevailing East Australian Current to spawn, with eggs and larvae transported southward to higher latitude nursery habitats (Suthers et al., 2011).

4.2 | Age composition and mortality

There was no observed general increase in the mean FL and age of *S. robusta* with increasing depth, which is consistent with that reported for the western population. This contrasts the situation for other coastal sillaginids, including *S. bassensis* (Hyndes & Potter, 1996) and *Sillaginodes punctata* (Hyndes et al., 1998) and many teleosts in general (Macpherson & Duarte, 1991), for which larger and older individuals inhabit deeper depths. The dominance of young fish (1–3 years) in the age compositions also concurs with previous accounts for the species (Butcher & Hagedoorn, 2003; Hyndes & Potter, 1996) and is typical of other harvested sillaginids, including *S. japonica* (Yokota et al., 1999), *S. aeolus* (Rahman & Tachihara, 2005), banded whiting *S. vittata* McKay, 1985 and western trumpeter whiting *S. burrus* Richardson, 1842 (Hyndes, Potter, & Hesp, 1996) and *S. maculata* (Kendall & Gray, 2009). The dominance of 1- and 2-year-old *S. robusta* at Newcastle compared to 2- and 3-year-olds at Yamba was probably latitude-related, as argued above for observed longevity.

The truncated longevity of *S. robusta* at Newcastle also resulted in higher estimates of *M*, *Z* and *F* compared to Yamba. Nevertheless, estimates of *E* were similar across both locations, although *E* was $>M$ at Yamba, whereas both values were equivalent at Newcastle. Our values of *Z* (>1.61), *F* (>1.15) and *E* (>0.71) were greater than those reported (*Z* = 1.24, *F* = 0.58, and *E* = 0.47) for the species by Butcher and Hagedoorn (2003). This could potentially be due to a combination of factors including (i) the previous estimates were made during the early years of the fishery (1991–1995) and potentially prior to any significant fishery-associated impacts, and (ii) the effects of sustained levels of harvesting of the species in our study area (Flood et al., 2014).

Natural mortality determination is an important, but difficult, life history parameter to estimate for exploited fish populations (Ricker, 1975; Liang & Pauly, 2017; Sippel, Lee, Piner, & Teo, 2017). Calculations of *F* and *E* and other stock and yield parameters are sensitive to changes in *M*, which can greatly influence stock assessment outcomes and subsequent management decisions (Newman et al., 2000; Sippel et al., 2017). Although the four estimation methods we used provided concordant estimates of *M* and corresponding values of *F* and *E* at each separate location, it is generally recommended that assessment studies incorporate a range of mortality estimation methods as a precautionary approach and to improve certainty, particularly in data-poor fisheries as studied here.

TABLE 2 Mortality and exploitation rate estimates of *Sillago robusta*. (a) Age-based catch-curve estimates of instantaneous rates of total mortality (Z) and annual total mortality rate (A) of *S. robusta* at each depth strata (shallow: 11–30 m), mid (31–60 m), deep (61–90 m) over the inner continental shelf waters at Yamba (29°26'S, 153°20'E) during 2006 and 2007, and Newcastle (32°55'S, 151°45'E) during 2007. Z , instantaneous rate of total mortality; SE , standard error; r^2 , coefficient of determination; A , annual total mortality rate given as the percentage of the population that dies each year. (b) Estimates of natural mortality (M) of *S. robusta* based on the four estimation methods and the corresponding calculated levels of fishing mortality (F) and exploitation rate (E) based on the minimum and maximum estimates of M of *S. robusta* captured across the three sampled depth ranges (11–90 m) over the inner continental shelf waters at Yamba (29°26'S, 153°20'E) in 2006 and 2007 and Newcastle (32°55'S, 151°45'E) in 2007. Z , instantaneous rate of total mortality; M , natural mortality; F , fishing mortality; E , exploitation rate

Location/Depth	Z	SE	r^2	A (%)
(a)				
Yamba 2006				
Shallow	1.55	0.04	.99	79
Mid	1.76	0.05	.99	83
Deep	2.01	0.08	.99	87
All depths	1.61	0.04	.99	80
Yamba 2007				
Shallow	1.87	0.04	.99	85
Mid	1.48	0.04	.99	77
Deep	2.11	0.01	.99	88
All depths	1.72	0.02	.99	82
Newcastle 2007				
Shallow	2.61	0.30	.98	93
Mid	NA	–	–	
Deep	NA	–	–	
All depths	2.70	0.27	.98	93
Location & Year				
	Yamba 2006	Yamba 2007	Newcastle 2007	
(b)				
Total mortality (Z)	1.61	1.72	2.70	
Natural mortality (M)				
Hoenig (1983)	0.42	0.42	0.70	
Hewitt and Hoenig (2005)	0.42	0.42	0.71	
Quinn & Derisio (1999)	0.46	0.46	0.77	
Pauly (1980)	0.43	0.43	NA	
Fishing mortality (F)				
F (minimum M)	1.19	1.30	2.00	
F (maximum M)	1.15	1.26	1.93	
Exploitation rate (E)				
E (minimum M)	0.74	0.76	0.74	
E (maximum M)	0.71	0.73	0.71	

4.3 | Fishery and climate implications

In this current study the estimates of F and E were greater than M , indicating that populations of *S. robusta* sampled here were heavily fished. Moreover, the percentage of each population that died each year (A) was considerable across both location, above

80%. Although extended harvesting of fish populations at exploitation levels >0.5 may not be sustainable (Patterson, 1992), the current levels of harvesting of eastern *S. robusta* are reported to be viable and not impacting recruitment levels (Flood et al., 2014). Nevertheless, periodic age-based monitoring of the population is warranted.

The warming of ocean waters along eastern Australia has resulted in a strengthening of the poleward-flowing East Australian Current and southward shifts in the distributions of several teleost and invertebrate species (Last et al., 2010; Lough & Hobday, 2011). Given the identified latitudinal plasticity in growth and length-at-age, it is plausible that the population distribution and demographics of *S. robusta* could similarly shift. For example, the longevity and proportion of older *S. robusta* at higher latitudes (such as Newcastle) could increase with further ocean warming. The data presented here and in Gray, Barnes, van der Meulen et al. (2014) provide a base to assess future fishery- and climate-associated changes in the population demographics of east Australian *S. robusta*.

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