Reproduction, growth and mortality of the exploited sillaginid, *Sillago ciliata* Cuvier, 1829

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Summary

The goal of this study was to examine the age and size composition, growth, reproductive biology and mortality of *Sillago ciliata* Cuvier, 1829 in one of the largest estuarine commercial fisheries in south-eastern Australia. The study also aimed to present a qualitative comparison of latitudinal variations in some of these characteristics along the eastern Australian coastline. The sampled population contained fish aged up to 10 years with a maximum size of 39.2 cm fork length (L_F), and was dominated by 1–5 year olds. Sexual divergence in both the age and size structure of the population was recorded. Female *S. ciliata* grew slightly faster and attained a greater maximum size ($L_\infty = 33.79$ cm L_F, $k = 0.50$ year^{-1} and $t_0 = -0.57$ years) than males ($L_\infty = 29.73$ cm L_F, $k = 0.49$ year^{-1} and $t_0 = -0.67$ years). Females also matured at a significantly larger size (19.13 cm) and older age (1.63 years) than males (size: 17.07 cm, age: 1.10 years). Reproductive activity was highest between September and March. There were no differences between males and females in terms of mortality rate; the estimated total population, natural and fishing mortality rates were $Z = 0.64$, $M = 0.42$ and $F = 0.22$, respectively. Although these mortality rates suggest that *S. ciliata* in the Clarence River are relatively resilient to current rates of exploitation, regular monitoring of their commercial and recreational catch as well as their population structure is recommended in order to maintain sustainable fisheries. Potential latitudinal shifts in the spawning period, age structure and growth of *S. ciliata* along eastern Australia were also revealed.

Introduction

Members of the family Sillaginidae (whiting) occur throughout the coastal and estuarine waters of the Indian and western Pacific oceans, where they form the basis of many important commercial, recreational and artisanal fisheries (McKay, 1992; Sulistiono et al., 1999; Rahman and Tachihara, 2005a; Butcher et al., 2006; Kendall and Gray, 2009). In eastern Australia, *Sillago ciliata* Cuvier, 1829 (sand whiting) is one of most heavily exploited sillaginids (McKay, 1992; Butcher et al., 2006; Ochwada et al., 2008; Gray et al., 2011) due to its iconic status. This primarily estuarine and near-shore species is harvested by both the commercial and recreational fishing sectors of New South Wales (NSW), with annual retained quantities for these sectors estimated at 61–191 tonnes (t) (2004–2013) and 230–460 t (2000–2001), respectively (Henry and Lyle, 2003; Rowling et al., 2010; NSW DPI Commercial Catch Records). Local demographic information is required to better understand the potential impacts of continued exploitation of *S. ciliata*.

Distribution of *S. ciliata* in Australia extends from Cape York, Queensland through to southeastern Tasmania (Morton, 1985; Burchmore et al., 1988; McKay, 1992). Most of what is currently known about this species, however, stems from studies conducted in its northern ranges (e.g. Morton, 1985; Weng, 1986; Goodall et al., 1987). With the exception of methodological papers (e.g. Ochwada et al., 2008; Stocks et al., 2011), published quantitative work on the biology of *S. ciliata* within its central distribution (along the NSW coastline) is limited to studies on spatial and temporal patterns of reproduction and the species' general habitat associations (Cleland, 1947; Burchmore et al., 1988). For most of its geographic range, there is limited published information on *S. ciliata* growth and mortality.

A comprehensive understanding of *S. ciliata's* population structure and its patterns of reproduction, growth and mortality in NSW will provide essential information for resource assessment and assist in developing appropriate management strategies for local conservation of this highly sought-after species. For *S. ciliata* sampled from the Clarence River, which is one of the largest coastal rivers in NSW and has supported the state's largest estuarine fishery for *S. ciliata* over the past decade (Smith, 1996; NSW DPI Commercial Catch Records; Gray et al., 2000), this study aims to describe: (i) age and size structure; (ii) temporal reproductive patterns and reproductive maturity; (iii) growth rates; and (iv) mortality rates. The results are compared to those reported for populations of *S. ciliata* sampled elsewhere and since intra-specific latitudinal shifts in the biology and demography of other estuarine teleosts have been previously documented in several parts of the world (e.g. Conover, 1990; Present and Conover, 1992; Arruda et al., 1993; Vinagre et al., 2009; Gray et al., 2010), a qualitative comparison of latitudinal variation in some of the measured parameters is also explored at the scale of the eastern Australian coastline. Finally, the implications of the results are considered with regard to fishery management practices.

Materials and methods

Study area and sampling procedures

Sillago ciliata were sampled from the Clarence River (29.427°S, 153.372°E) on the north coast of NSW, which has a catchment area of ~22 700 km². Samples of *S. ciliata* were collected by researchers from vegetated, soft-sediment areas in the lower reaches of the Clarence River within 5 km of the river's mouth using multimesh gillnets (mesh size ranged from 44–120 mm), beach-seine (haul) nets (mesh size 20 mm) and angling techniques. Samples were collected during day and night periods on a monthly basis between September 2005 and September 2006 within one week prior to the full moon to avoid any bias associated with the full moon. Information on the place and date of capture was recorded for each sampled fish.

Processing of fish

Fork lengths (L_F) and total body weights (W_t) of all *S. ciliata* sampled were measured to the nearest 0.1 cm and 0.1 g, respectively. Gonads were macroscopically examined to enable determination of sex based on the presence of ovaries or testes. For sexed fish with intact gonads (n = 1852), the gonads were extracted and weighed to the nearest 0.1 g to obtain a gonad weight (W_g). Each gonad was assigned a reproductive stage based on similar characteristics as described in Hughes et al. (2008). Macroscopic stages of male and female fish were: immature (stage 1), developing or resting (stage 2), ripe (stage 3), running ripe (stage 4) or spent (stage 5). The sex of all juveniles sampled could not be determined and their reproductive stage was therefore assigned as stage 1. Sagittal otoliths were surgically removed, cleaned, dried and stored separately for each fish retained for analysis of growth (n = 1753). One of each pair of otoliths was randomly selected [i.e. chosen on the basis of a non-probabilistic sampling scheme in which elements are selected blindly (Lewis, 2004)] and embedded in resin so that a thin transverse section could be made through the core, perpendicular to the ototlith's longest axis. Sections were polished, mounted onto slides and viewed under a stereomicroscope at 2× magnification using reflected light against a black background.

Population structure

All statistical analyses described within this and the following sections were carried out in the open-source statistical package 'R' (Ihaka and Gentleman, 1996). Sex ratios were compared using a Chi-squared (χ^2) test ($\alpha = 0.05$). For each sex, an age-length-key (ALK) was constructed using aged fish and applied to all fish sampled to estimate the age structure of the sampled population (see section on age estimation for details on ageing). The ALKs for females and males were constructed using sub-samples of n = 932 and n = 862 aged fish, respectively. Sub-samples consisted of randomly selected fish from each length interval observed in the entire sample. Two-sample Kolmogorov–Smirnov (K–S) tests ($\alpha = 0.05$) were then used to compare size and age frequency distributions between sexes. The data for each sex's age and length

structures included half of the sampled juveniles (unsexed fish); inclusion of juveniles into a particular sex was done randomly.

Reproduction

Spawning Season. Gonadosomatic indices (I_G) were calculated using the equation:

$$I_G = 100 \times \left(\frac{W_g}{W_t}\right)$$

Monthly variations in the mean I_G and the proportion of reproductively active fish (≥stage 2) were used to estimate the spawning season using sexed fish.

Size and age at maturity. For fish sampled during the I_G-defined spawning season (defined as the period during which the highest average I_G values and the highest proportion of reproductively active individuals were observed), the proportion of mature (≥stage 2) fish within each 1 cm L_F category and year class was determined. Logistic curves were fitted to these data and used to estimate the size (L_F (cm)) and age (years) at which 50% of female and male fish sampled attained maturity (L_{Fm50} & A_{m50} respectively). Note that half of the juveniles sampled during the spawning season were included in the data used to construct the logistic curves for each sex.

A logistic regression model was developed to examine whether the factors L_F, Sex and the interaction between these factors were associated with the proportion of mature fish sampled. Maturity was treated as a binary variable (1 = mature, 0 = immature) in the model and the full original model took on the general form of:

$$LOGIT(\text{Maturity}) = \beta_0 + \sum_{i=0} \beta_i x_i$$

where β_0 was the vertical intercept and the β_is were the partial regression coefficients for each factor or the first-order interaction term x_i. The drop1() function in *R* was used to calculate and compare Akaike Information Criteria (AIC) values associated with the full original model and a reduced model that excluded the interaction term. When exclusion of the interaction term did not result in an improved AIC value, this meant that the term was essential to the model. For the final and most parsimonious model subsequently selected, the influence of each retained factor or interaction term on the proportional maturity of fish was examined using partial z-tests ($\alpha = 0.05$). These tested the null hypothesis that β_i for a particular factor or the interaction term was equal to zero. A similar logistic regression model was developed to examine whether the factors Age, Sex and the interaction between them were associated with the proportion of mature fish.

Growth

Age estimation. Completed visible opaque zones on the otoliths extracted from fish were counted along the radius of

each otolith from the core to the outer edge of the ventral lobe and used as estimates of age. The deposition of these opaque zones has been previously validated to occur annually for adult (legal sized) *S. ciliata* in southeastern Australia (Gray et al., 2000; Stocks et al., 2011). All extracted otoliths were aged without prior knowledge of sample details (i.e. L_F, sex, and date of capture). Ten percent of the samples were haphazardly selected and aged a second time, enabling calculation of the coefficient of variation (CV) between the first and second age readings using the equation:

$$CV = 100 \times \frac{\sqrt{\sum_{i=1}^{r} \frac{(x_{ij}-x_j)^2}{r-1}}}{x_j}$$

where x_{ij} was the *i*th age determination of the *j*th fish, x_j was the mean age estimate of the *j*th fish and *r* was the number of times each fish was aged (Chang, 1982; Campana et al., 1995). A mean CV across all fish that were secondarily aged was calculated to determine the precision of age estimates. The mean CV subsequently attained was 1.11%, which is within the accepted maximum reference point of 5% (Campana, 2001).

Age validation. Wild *S. ciliata* were collected from Botany Bay (33°59′S; 151°1.11′E) at the beginning of May 2003 using research beach-seine (haul) nets with stretched mesh sizes ranging from 5 to 20 mm. In total, 123 individuals ranging from 53 to 135 mm FL were captured and transported live in aerated containers to the aquaria facility at the Cronulla Fisheries Research Centre (30-min drive) where they were given a mild antibiotic bath (100 g/1000 litres oxytetracycline solution) to reduce the risk of infection from handling and transportation, and transferred into a 5000-L tank with flowthrough seawater maintained at near ambient water (water pumped directly from Port Hacking estuary) and air temperatures. Fish were monitored and fed high protein fish pellets once a day.

On 15 May 2003, all fish were immersed in an alizarin complexone bath (50 mg L^{-1} of seawater) for a period of 24 h to stain their otoliths. Every 4–6 weeks thereafter until February 2005, five to ten individuals were collected from the tank and euthanized to examine their otolith growth subsequent to the alizarin mark. Sagittal otoliths of each sampled fish were removed and processed as described above. The number of completed opaque zones occurring subsequent to the alizarin band was counted and the distance from the alizarin band to the otolith edge was measured and, if present, the distance from the otolith core to the first opaque zone was also measured. All measurements were done on the outer side of the sulcus, on the ventral lobe.

Growth modelling. The von Bertalanffy growth (VBG) function was fitted to the L_F at age data using the equation:

$$L_t = L_\infty[1 - e^{-k(t-t_0)}]$$

where *t* was the age in years, L_t the fork length (cm) at age *t*, t_0 the theoretical age of the fish in years when they had no

length, L_∞ the asymptotic fork length (cm), and *k* the rate at which the curve approached L_∞ (year^{-1}). Growth curves were developed for each sex (with half the sampled juveniles included in each sex) and the subsequent curves then compared among sexes, over equivalent ranges of age (0–10 years) and L_F (2.1–33.4 cm) (Haddon, 2001), using the analysis of residual sums of squares (ARSS) method ($\alpha = 0.05$) described by Chen et al. (1992).

Mortality

Estimates of the instantaneous rate of total mortality (Z) were made for each sex using the age-based catch curve method (Beverton and Holt, 1975; Ricker, 1975). These analyses assumed that: (i) the most abundant age class was fully recruited in each population, (ii) catchability of fish of different sizes, recruitment and growth were constant through time, and (iii) growth was asymptotic. The natural logarithm of the number of fish in each age class (N_t) was plotted against the corresponding age class (t) and a linear regression fitted. The regressions were truncated at the age class preceding the most abundant age class. Total mortality was estimated from the descending slope, b. Standard error (SE) and R^2 values were calculated for each regression. An instantaneous natural mortality rate (M) was also estimated using the method described by Hoenig (1983) for 84 stocks of teleosts and was based on maximum age. The equation used for natural mortality was:

$$\ln(M) = 1.46 - 1.01 \ln(t_{max})$$

where t_{max} was the maximum age. Fishing mortality (F) was then estimated as the difference between |Z| and |M|.

A one-way analysis of covariance (ANCOVA) ($\alpha = 0.05$) was used to examine sexual variation in total mortality. The natural logarithm of N_t was the dependent variable, t was the covariate and sex was the factor. The assumption that regressions were homogenous among sexes was tested using a full ANCOVA that analysed the factor by covariate interaction term (which, if significant, indicated heterogeneity) (Underwood, 1997; Quinn and Keough, 2002), and the regressions were shown to be homogeneous ($F = 4.29$, $P = 0.06$ d.f. = 1). Bartlett's test showed that the variances were homogenous ($K = 0.01$, $P = 0.92$, d.f. = 1) (Underwood, 1997) and residual and quantile-quantile plots of the ANCOVA model indicated adequate normality of the data. Note that half of the sampled juveniles were again included in each sex when fitting the linear regressions.

Results

Population structure

A total of 2119 *S. ciliata* were collected and retained for analysis. The number of females sampled (966) was statistically similar to the number of males sampled (891) ($\chi^2 = 3.03$, d.f. = 1, $P = 0.08$). Significantly fewer juveniles (262) were sampled compared to males and females ($\chi^2 = 423.26$, d.f. = 2, $P < 2.20 \times 10^{-16}$). Size frequency distributions showed significant variation among sexes (K–S

test: $D = 0.36$, d.f. $= 1$, P $< 2.2 \times 10^{-16}$), with the average ($\pm$SE) L_F of females being 28.08 ± 0.17 cm, and that of males 24.15 ± 0.16 cm (Fig. 1).

Although each sex was predominantly composed 1- to 5-year-old fish, the corresponding age structures showed significant variation among sexes (K–S test: $D = 0.08$, d.f. $= 1$, P $= 6.49 \times 10^{-4}$). This was due to fewer 1- and 2-year-olds and more 3- and 4-year-olds among female fish relative to male fish (Fig. 2). The lowest number of individuals was observed for fish aged ≥ 6 years in each sex (Fig. 2).

Reproduction

Spawning period. The highest average I_G values were observed between September and April for females, and between August and March for males (Fig. 3). Peaks in average I_G occurred during November for females ($6.49 \pm 0.49\%$) and during September for males ($5.18 \pm 0.10\%$) (Fig. 3). The proportion of females with reproductively active gonads was greatest (87.8–100%) between September and March (Fig. 4a). Similarly, the proportion of males with reproductively active gonads was greatest (80.8–100%) between August and April (Fig. 4b).

Size and age at maturity. For the purpose of determining size and age at maturity, the spawning period was estimated to fall between September and March for females and August and March for males. The lowest AIC value for the logistic regression models used to examine the influence of L_F and Sex on proportional maturity was observed for the model that included both L_F and Sex as factors but omitted the interaction term between these factors, suggesting that sex and L_F influenced proportional maturity independently. Partial z-tests on this parsimonious model indicated the probability that $\beta_i = 0$ was significant for both L_F and Sex (Table 1a). Separate logistic curves were therefore fitted for each sex to assess size at maturity (Fig. 5). The logistic curves showed that female *S. ciliata* mature at between 15 and 25 cm L_F, with 50% maturity attained at an L_F of 19.13 ± 0.40 cm (Fig. 5a). Male fish, on the other hand, matured at between 10 and 21 cm L_F, with 50% maturity attained at an L_F of 17.07 ± 0.54 cm (Fig. 5b). The lowest

AIC value for the logistic regression models used to examine the influence of Age and Sex on proportional maturity was again observed for the model that excluded the interaction term. The partial z-tests indicated the probability that $\beta_i = 0$ was significant for both Age and Sex (Table 1b). The logistic curves showed that 50% of females and males attained maturity at 1.63 ± 0.08 and 1.10 ± 0.06 years of age, respectively.

Age validation and growth

The alizarin stain was visible as a thin red band in the sectioned otoliths of all *S. ciliata*. Prior to that alizarin band, 79 individuals had 0, 43 had 1 and 4 had 2 opaque zones. The first opaque zone deposited after the alizarin band was visible between November and December, whereas a second opaque zone was visible between the following September to January (Fig. 6). The mean distance from the otolith core to the first opaque zone was 0.65 (± 0.11 SD) mm.

The ARSS test revealed that growth of male and female fish differed significantly ($F_{3,1949} = 142.05$, P $< 1.00 \times 10^{-04}$). Separate growth curves were therefore fitted for each sex (Fig. 7). Female *S. ciliata* reached a mean size of 17.25 cm L_F at 1 year, 28.36 at 3 years and 31.81 cm at 6 years, after which growth slowed dramatically (Fig. 7). Growth was slower for males, which reached mean sizes of 15.75 cm L_F, 24.99 cm L_F and 28.83 at 1, 3 and 6 years of age, respectively (Fig. 7). Growth rates of males also declined beyond 6 years of age (Fig. 7).

Mortality

Estimated total mortality of females was $Z = 0.79 \pm 0.07$ ($R^2 = 0.96$), and that of males was $Z = 0.58 \pm 0.06$ ($R^2 = 0.93$). Total mortality rates were not statistically different between sexes (ANCOVA: $F = 2.01$, P $= 0.18$ d.f. $= 1$). A single linear regression was therefore fitted to estimate overall total mortality, which was $Z = 0.64 \pm 0.05$ ($R^2 = 0.91$) based on a maximum age of 10 years (Fig. 8). Overall natural mortality was $M = 0.42$, and overall fishing mortality rate was $F = 0.22$.
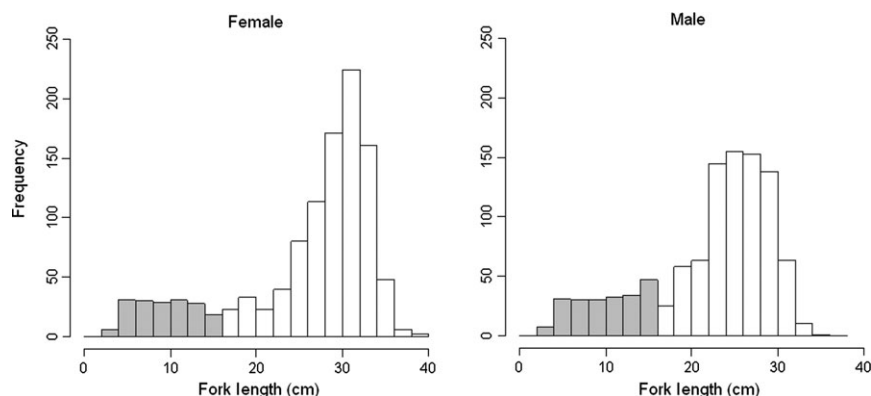

Fig. 1. Length-frequency distribution of femaleand juvenile *Sillago ciliata* (n = 1097) and male and juvenile *S. ciliata* (n = 1022), Clarence River (NSW, Australia), September 2005 – September 2006. Length classes containing juveniles marked in grey
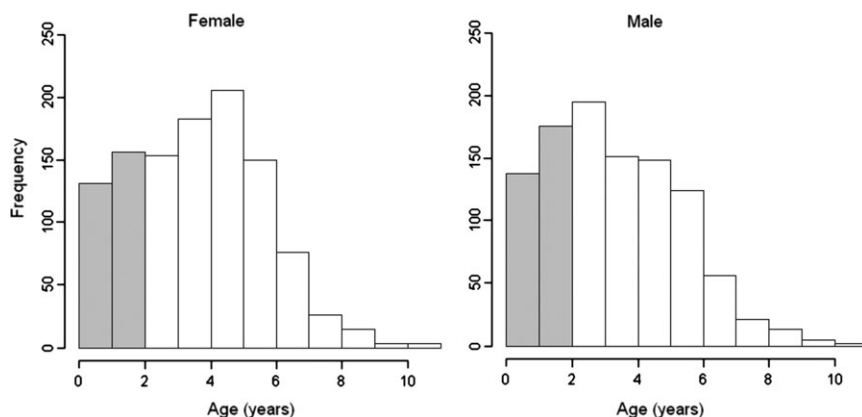
Fig. 2. Age-frequency distributions based on age-length-keys of female and juvenile *Sillago ciliata* (n = 1105) and male and juvenile *S. ciliata* (n = 1031), Clarence River (NSW, Australia), September 2005 – September 2006. Age classes containing juveniles marked in grey
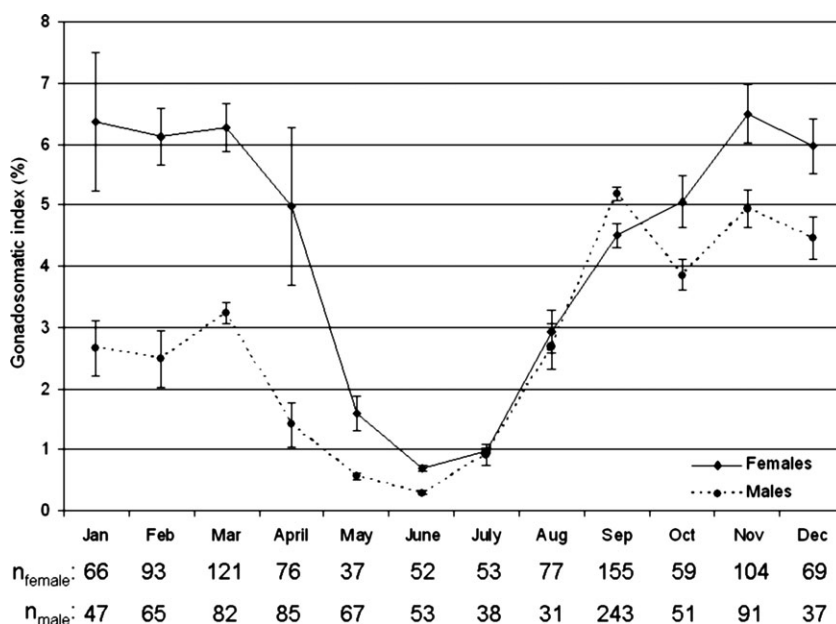

	Jan	Feb	Mar	April	May	June	July	Aug	Sep	Oct	Nov	Dec
n_{female}:	66	93	121	76	37	52	53	77	155	59	104	69
n_{male}:	47	65	82	85	67	53	38	31	243	51	91	37

Fig. 3. Average (±SE) gonadosomatic indices for female (n = 962) and male (n = 890) *Sillago ciliata*, Clarence River (NSW, Australia), September 2005 – September 2006

Discussion

Population structure

This study showed that there were similar proportions of male and female *Sillago ciliata* within the Clarence River. This suggests similar mortality rates between the sexes across the population's entire size range, a notion confirmed by the present comparison of total mortality between the sexes. These findings contrast those reported for *S. ciliata* found elsewhere, where male fish were shown to occur at significantly higher numbers than females (Morton, 1985; Burchmore et al., 1988). The sexual variation in size structure observed here was likely driven by the fact that the most abundant size classes for females ranged from 26–32 cm while those of males ranged from 22–28 cm. These findings are somewhat supported by those reported by Morton (1985), who found more large females within populations of *S. ciliata* in Moreton Bay and suggested that these patterns may be caused, in part, by sex-based disparities in growth rates.

Age structure of the population differed significantly among sexes and the data suggests that this was attributable to sexual variation in age frequencies occurring between 1 and 4 years of age. Female dominance in the population began after 2 years of age, which is also when *S. cillata* generally mature (Cleland, 1947; Goodall et al., 1987). This pattern coincides with a previous study which showed that there were more female adults than male adults in a population of *S. ciliata*, possibly due to faster female growth rates (Burchmore et al., 1988). This further supports the explanation given above for sexual variation in size structure. Overall, the population was dominated by 1- to 5-year-old fish. This dominance of young fish has also been previously reported for *S. ciliata* (Stocks et al., 2011) and other sillaginids in Australia and Japan (Hyndes and Potter, 1996, 1997; Sulistiono et al., 1999; Butcher and Hagedoom, 2003; Rahman and Tachihara, 2005a; Kendall and Gray, 2009).

Reproduction

Reproductive activity of *S. ciliata* was greatest during early-spring to mid-autumn between September and March. This
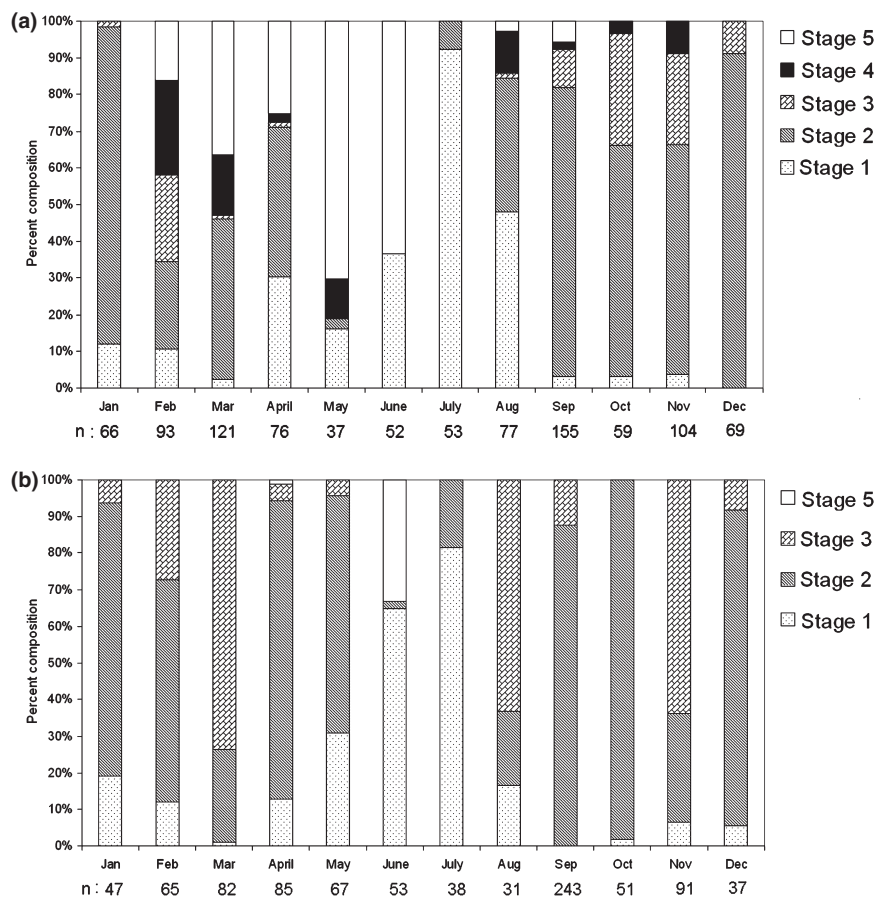
Fig. 4. Monthly proportions of reproductively immature (stage 1 gonads) and mature (≥stage 2 gonads) (a) female (n = 962) and (b) male (n = 890) *Sillago ciliata*, Clarence River (NSW, Australia), September 2005 – September 2006

Table 1
Partial *z*-tests used to examine effect of (a) fork length (L_F) and sex on maturity of *Sillago cilata* (n = 1283) and (b) age and sex on maturity of *S. cilata* (n = 1939) as estimated from respective regression models (i) logit (Maturity) = $\beta_0 + \beta_1 L_F + \beta_2$ Sex and (ii) logit (Maturity) = $\beta_0 + \beta_1$ Age + β_2 Sex. Analysed *S. cilata* were sampled from Clarence River (NSW, Australia), September 2005 – September 2006. Given are the models' intercept (β_0) and its standard error (SE), as well as the partial regression coefficients and SEs for L_F or Age (β_1) and the regressor of the categorical variable Sex (β_2). The probability that $\beta_i = 0$ for the intercept and each factor in the models (P(>|z|)) is also given

	β_i (SE)	P(>|z|)
(a)		
Intercept	$\beta_0 = -13.41$ (1.49)	$<2.00 \times 10^{-16}$
L_F	$\beta_1 = 0.70$ (0.07)	$<2.00 \times 10^{-16}$
Sex$_{Male}$	$\beta_2 = 2.01$ (0.43)	2.42×10^{-06}
(b)		
Intercept	$\beta_0 = -2.21$ (0.15)	$<2.00 \times 10^{-16}$
Age	$\beta_1 = 1.34$ (0.06)	$<2.00 \times 10^{-16}$
Sex$_{Male}$	$\beta_2 = 0.78$ (0.14)	3.63×10^{-08}

matches the reproductive season reported for *S. ciliata* further north in Moreton Bay (September to March) (Morton, 1985), but is longer than that reported for a population found further south in Botany Bay (December to April) (Burchmore et al., 1988). This difference in the reproductive period may be associated with geographic differences in envi-

ronmental conditions (e.g. water temperature, photoperiods). The reproductive season of the present population is similar to that documented for other sillaginid species found elsewhere in Australia and coincides with periods of increasing or maximum water temperatures and photoperiods, which may be a cue for reproductive development and activity in sillaginids (Hyndes and Potter, 1996; Kendall and Gray, 2009).

The size and age at which *S. ciliata* matured differed between sexes, with the L_{Fm50} and A_{m50} of females being greater than that of males. This pattern is similar to that previously reported for other sillaginids in other parts of Australia and Japan (Hyndes et al., 1996; Rahman and Tachihara, 2005b), but is in contrast to findings for both *S. ciliata* and other sillaginids in Botany Bay that revealed similar sizes at maturity for males and females (Burchmore et al., 1988). In animals that exhibit sexually dimorphic maturation, such as that observed here, the sex that is larger or older at reproductive maturity may defer attainment of maturity because it requires more time to develop the physical, physiological or social attributes needed to breed successfully (Bisazza, 1993; Stamps and Krishnan, 1997). In some female fish, fecundity (number of eggs per female) increases significantly with increasing size (Bisazza, 1993). Thus maturation at a larger size and older age may increase a female's reproductive output and chances of breeding
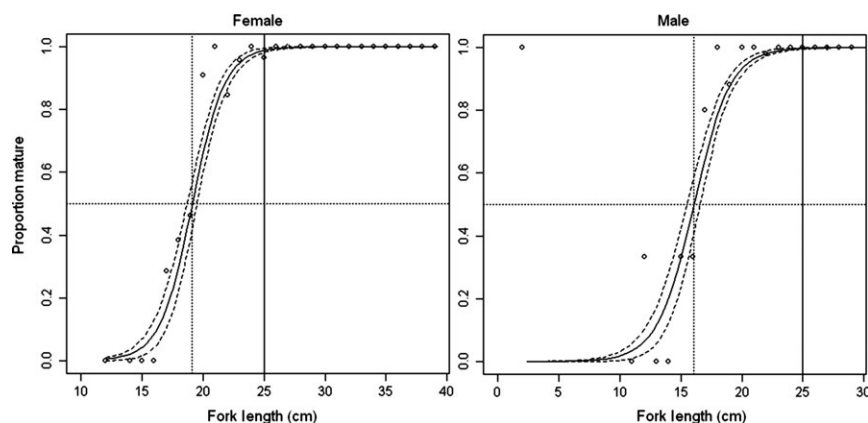
Fig. 5. Reproductive maturity data with fitted logistic curves (solid curve) for female (n = 664) and male (n = 619) *Sillago ciliata*, Clarence River (NSW, Australia), September 2005 – September 2006. Intersection of dashed vertical and horizontal lines = estimate of fork length (cm) at 50% maturity; solid vertical line = minimum legal length (~25 L_F cm) for *S. ciliata* in NSW, Australia
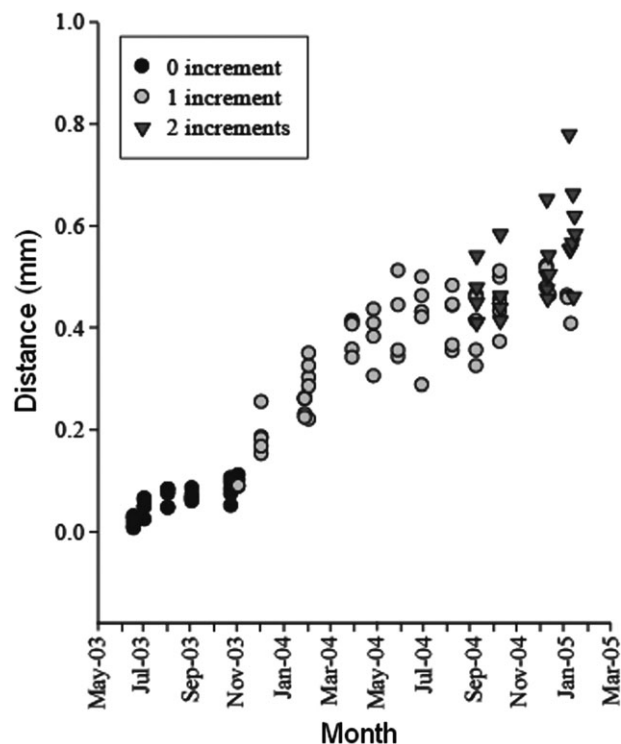

Fig. 6. Changes in distance (mm) between bands resulting from alizarin complexone stains and the edge of the otoliths showing timing of opaque zone formation for wild-caught *Sillago ciliata* housed in aquaria facilities, Cronulla Fisheries Research Centre, NSW (Australia), May 2003 – February 2005

successfully (Cowx, 1983). For both sexes, estimated L_{Fm50} values were less than those reported for *S. ciliata* in Botany Bay (L_{Fm50} = 24) (Burchmore et al., 1988). This difference may be related to spatio-temporal variations in environmental conditions or differences in sampling methods.

Age validation and growth

Opaque growth zones on the otoliths of juvenile *S. ciliata* kept in aquaria were deposited annually. This, together with previ-

ous observations of opaque zones in adult fish as annuli, validates their use for estimating the age of *S. ciliata*. Data indicate that the 1st opaque zone is first visible slightly earlier (November/December) than successive (i.e. 2 +) opaque zones (September to January). This is probably due to younger fish growing faster and therefore depositing an opaque growth zone that can be observed earlier. Opaque growth zones are generally formed over winter during periods of slow growth whereas translucent growth zones represent periods of faster growth over summer and autumn. The general austral spring/summer timing of the completion of opaque zone growth is in general agreement with similar validation studies on a range of estuarine/coastal fish in southeast Australia (Stewart and Hughes, 2007; Hughes et al., 2008; Kendall and Gray, 2009).

Individual *S. ciliata* grew quickly, attaining 28 (female) and 25 (male) cm L_F in 3 years. The data suggests that the life span of *S. ciliata* in the Clarence River is short, attaining a maximum age of 10 years and a maximum size of about 39.2 cm. Although few published studies have investigated the growth of *S. ciliata* in detail, especially using the von Bertalanffy growth function (but see Stocks et al., 2011), Cleland (1947) reported a maximum age of 22 years and a maximum size of 45 cm for *S. ciliata* in Queensland, and a maximum age and size of 18 years and 43 cm for *S. ciliata* in NSW. These disparities relative to the present data may be due to changes in longevity induced by fishing pressure within the Clarence River. Fishing has been shown to truncate the age of numerous teleosts worldwide (Berkley et al., 2004; Hsieh et al., 2006; Balazik et al., 2010; Stewart, 2011); the *S. ciliata* population in the Clarence River experienced among the highest levels of commercial fishing pressure during the years leading up to and during this study (annual landings between 2002/2003 and 2006/2007:17.4–34.6 t) relative to other estuaries in NSW (NSW DPI Commercial Catch Records). Although *S. ciliata* is harvested by the commercial gill-netting fishery in many NSW estuaries, the largest proportion of its commercial harvest in the Clarence River and other estuaries in the state comes from the beach-seine (haul) fishery. Like many other methods of fishing that are capable of capturing larger and therefore more valuable or coveted fish, this method is likely to truncate the age

Fig. 7. Fork length (cm) at age (years) data for female (n = 905) and male (n = 848) *Sillago ciliata*, Clarence River (NSW, Australia), September 2005 – September 2006. Fitted von Bertalanffy growth curves and simulated growth parameters (±SEs) also shown

$L_\infty = 33.79 \pm 0.32$ cm L_F
$k = 0.50 \pm 0.02$ year^{-1}
$t_0 = -0.57 \pm 0.03$

$L_\infty = 29.73 \pm 0.31$ cm L_F
$k = 0.49 \pm 0.02$ year^{-1}
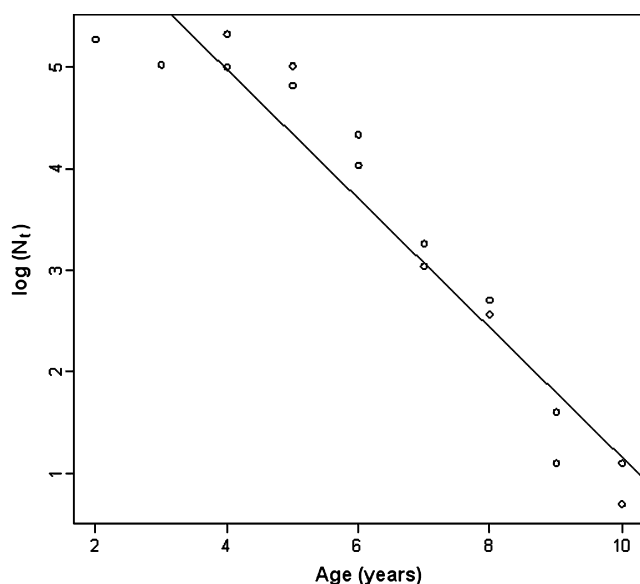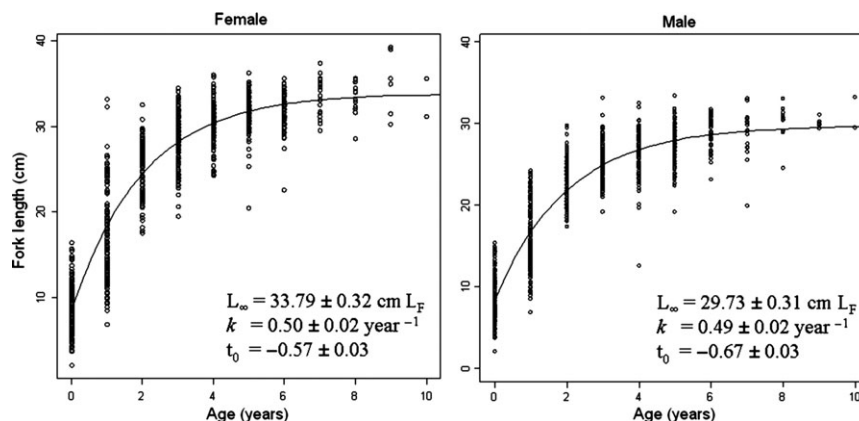$t_0 = -0.67 \pm 0.03$

Fig. 8. Linear regression of age (years) of *Sillago ciliata,* Clarence River (NSW, Australia), September 2005 – September 2006, as plotted against the natural logarithm of the number of fish in each age class (N_t). This regression was used to estimate overall mortality rate

structure of a species over time through the gradual removal of larger, older fish (Broadhurst et al., 2006; Steer et al., 2011; Stewart, 2011). Historical recreational harvest of the *S. cilliata* is likely to have played a similar role in truncating age structures. Even so, differences in aging procedures among studies and geographic differences in environmental characteristics may have contributed to the regional differences described above in the maximum age and size of *S. ciliata*. Other sillaginid species have been shown to attain a maximum age of up to 12 years (*S. maculata*) in eastern Australia (Kendall and Gray, 2009) and up to 14 years (*Sillaginodes punctata*) in western Australia (Hyndes et al., 1998). The von Bertalanffy growth function parameter estimates reported here suggest that *S. ciliata* in the Clarence River approach their theoretical maximum size at slower

rates and attain higher maximum sizes than those reported for other sillaganid species examined in Japan and other parts of Australia (see Kendall and Gray, 2009).

Female *S. ciliata* grew faster than males, supporting some of the hypotheses discussed earlier regarding size and age structures. Sexual divergence in growth rate is common among teleosts and consistent with results reported for other *S. cilata* populations (Stocks et al., 2011) and other sillaginid species (Hyndes et al., 1998; Rahman and Tachihara, 2005a; Kendall and Gray, 2009). This pattern may be linked to differences in the reproductive potential of male and female fish. Continued fast growth beyond maturity may be unnecessary in males since the gametes of a single male fish are capable of fertilizing the eggs of several females irrespective of the male's size (Cowx, 1983). In contrast, females may need to keep growing beyond sexual maturity to maximise their potential fecundity, as this is often directly linked to body size (e.g. Cowx, 1983; Coates, 1988; Morita and Takashima, 1998).

Mortality

Estimates derived here indicate that fishing mortality is less than the natural mortality for *S. ciliata*. In combination with this species' short life-span, fast growth and early attainment of reproductive maturity, these relative mortality rates suggest that the population in the Clarence River is currently resilient to present levels of fishing pressure. The natural and fishing mortality rates estimated here for *S. cilliata* are less than those estimated for the offshore sillaginid *S. robusta* in southern Queensland ($M = 0.7$, $F = 0.54$) (Butcher and Hagedoom, 2003).

Broader latitudinal observations

Juxtaposition of the current results with those reported in other studies of *S. ciliata* reveals a number of potential latitudinal trends in the biology and demography of this species along the east Australian coastline. These patterns are summarised in Table 2. Of particular note are the trends with increasing latitude towards a (i) delayed and contracted spawning period; (ii) narrower range of dominant age classes; (iii) slight decrease in maximum age; and a (iv) decrease in growth rate. Studies on other estuarine teleosts have previ-

Table 2
Qualitative comparison of selected biological and demographic characteristics of eastern Australian *Sillago ciliata* populations reported in the current study and published literature

Estuary (Latitude; longitude)	Sex ratios	Spawning period	Maturity	Age structure	Max. age & size	Mean standardized growth index
Moreton Bay (27.18° S; 152.25°E)	Male > Female (Morton, 1985)	Sep-Mar (Morton, 1985)				
Clarence River (29.43° S; 153.37°E)	Male = Female (Current Study)	Sep-Mar (Current Study)	L_{Fm50}; Female = 19.13 cm; Male = 17.07 cm. A_{m50}: Female = 1.63 years; Male = 1.10 years. (Current Study)	Dominance of 1–5 year olds (Current Study). Dominance of 2–5 year olds (Stocks et al., 2011)	Age = 10 years; L_F = 39.2 cm (Current Study; Stocks et al., 2011).	~0.7 (Stocks et al., 2011)
Wallis Lake (32.17° S; 152.51°E)				Dominance of 3–5 year olds (Stocks et al., 2011)	Age = 12 years; (Stocks et al., 2011).	~0.075 (Stocks et al., 2011)
Botany Bay (34.00° S; 151.23°E)	Male > Female (Burchmore et al., 1988)	Dec-Apr (Burchmore et al., 1988)	L_{Fm50}; Female = Male = 24 cm. (Burchmore et al., 1988)		L_F = 40 cm (Burchmore et al., 1988)	
St Georges Basin (35.15° S; 150.59°E)				Dominance of 3–4 year olds (Stocks et al., 2011)	Age = 8 years; (Stocks et al., 2011).	~0.125 (Stocks et al., 2011)
Wallaga Lake (36.77° S; 150.08°E)				Dominance of 3–4 year olds (Stocks et al., 2011)	Age = 8 years; (Stocks et al., 2011).	~0.30 (Stocks et al., 2011)

ously documented a shift towards an earlier spawning season at lower latitudes; these patterns have been attributed to latitudinal changes in photoperiod, temperature or the synergetic, concomitant effects of these factors which trigger spermatogenesis and oocyte development (Secor and Houde, 1995; Vinagre et al., 2009; Walsh et al., 2011). Latitudinal shifts in the growth of fish have similarly been related to changes in temperature, with some suggesting that fish found in cooler waters at high latitudes are faced with shorter growing seasons and a limited opportunity for growth (Garvey and Marschall, 2003; Vinagre et al., 2009), which could lead to smaller maximum sizes and ages and an observation of fewer fish in higher classes of age and size. Accordingly, Stocks et al. (2011) reported a decrease in eastern Australian water temperatures with increasing latitude and a significant, positive relationship between temperature and growth over the lifetime of *S. ciliata*. It should be noted, however, that the majority of the latitudinal comparisons described here are merely qualitative and somewhat cursory due to the different methodologies applied among the studies summarised in Table 2 and the absence of statistical evaluation. Future standardised studies should endeavour to quantitatively test hypotheses regarding latitudinal differences in the biology and demography of *S. ciliata*, especially in light of the higher water temperatures expected under projected climate change scenarios, which could cause the spawning period, maximum sizes/ages and thus maturity of *S. ciliata* found at higher latitudes to closely resemble those of their lower-latitude-counterparts. Such changes would necessitate adaptation of fisheries management strategies for *S. ciliata*.

Implications for management

The L_{Fm50} (17–19 cm L_F) estimated here suggests the current minimum legal length set for retaining *S. ciliata* in NSW (approx. 24.50 cm L_F) allows the majority of fish in the Clarence River to spawn at least once before they can be legally harvested, thereby protecting some spawning individuals from fishing mortality. The mortality estimates derived here indicate that fishing mortality is less than natural mortality for *S. ciliata*. Based on these findings, the population in the Clarence River appears to be relatively resilient to present levels of fishing pressure (Musick, 1999; Reynolds et al., 2005; Grandcourt et al., 2006). The reported rates of mortality also suggest that the characteristics of the present population of *S. ciliata* most closely matches the mortality rate criteria of a 'fully fished' stock (Scandol and Rowling, 2007). Over time however, exploitation rates of *S. ciliata* could potentially increase given that it is highly sought-after by both commercial and recreational fishers in eastern Australia. Regular monitoring and assessment programs for local *S. ciliata* populations are therefore required to determine potential changes in the condition of the stocks.

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