



Depth interactions and reproductive ecology of sympatric Sillaginidae: *Sillago robusta* and *S. flindersi*

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ABSTRACT: This study examined whether differences existed in the depth distributions and reproductive strategies of the co-occurring *Sillago robusta* and *S. flindersi* in coastal waters off eastern Australia. Marked spatial and temporal dissimilarities in demography and reproduction were observed between the 2 species, with *S. robusta* being more abundant in the shallow (15–30 m) strata and *S. flindersi* in the mid (31–60 m) strata, with neither species being consistently abundant in the deep (61–90 m) strata. The size composition of *S. robusta* was similar across depths, but smaller and immature *S. flindersi* predominantly occurred in the shallow strata, with larger and mature individuals occurring deeper. These data indicate partitioning of habitat resources, which may aid species coexistence. Both species potentially spawned year-round, which is probably an adaptation to the region's dynamic coastal environment. However, a greater proportion of *S. robusta* was in spawning condition between September and March, whereas *S. flindersi* displayed no such temporal pattern. Maturity ogives differed significantly between sexes and locations for both species. Both species displayed similar ovarian development, with females having multiple concurrent oocyte stages, indicating potential multiple spawning events as evidenced in other Sillaginidae. For both species, estimated batch fecundity increased with fish length, but *S. robusta* had a greater fecundity at any given length than *S. flindersi*. In contrast, *S. flindersi* potentially produced larger-sized eggs and invested greater energy into gonad development than *S. robusta*, indicating the 2 species have evolved slightly different reproductive strategies. Despite this, both species are subjected to substantial trawl fisheries, which may have already impacted their reproductive ecologies.

KEY WORDS: Life history · Habitat partitioning · Population structure · Reproduction · Maturity · Spawning · Fishery exploitation

INTRODUCTION

Knowledge of the life history characteristics of co-occurring species is fundamental to understanding biotic processes that influence structure and maintenance of assemblages of organisms (Schoener 1974,

Ross 1986, Roff 1992). Closely related teleost species that coexist often display different life history characteristics, such as reproductive and recruitment strategies, diets and small-scale distributions and abundances (Ross 1977, Roff 1991, Hyndes et al. 1997, Genner et al. 1999, Colloca et al. 2010). Such strate-

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gies maximise partitioning of resources, minimise the potential for interspecific competition, and may contribute to the coexistence of different assemblages and thus affect assemblage structure (Schoener 1974, Werner et al. 1977, Ross 1986).

Members of the teleost family Sillaginidae (whiting) inhabit subtropical and temperate coastal shelf and estuarine waters of the Indian and Western Pacific Oceans (McKay 1992, www.fishbase.org). The family contains 31 species, of which 13 occur in Australian waters, with 6 of these distributed along the east coast (McKay 1992). Sillaginids display a high degree of similarity in coloration and external morphology, having slender elongate fusiform-shaped bodies and long conical snouts. Most species attain maximum total lengths less than 40 cm and longevity under 12 yr (McKay 1992, Kendall & Gray 2009). Sillaginids are benthic carnivores that feed on small invertebrates such as polychaetes and crustaceans (Gunn & Milward 1985, Hyndes et al. 1997, Hajisamae et al. 2006) and can be a prominent component of soft-sediment benthic ichthyofaunas (Gray & Otway 1994, Chen et al. 2009, Gray et al. 2011, Nakane et al. 2013). Several species are important in commercial, recreational and artisanal fisheries (McKay 1992, Kailola et al. 1993, Gray & Kennelly 2003).

Life history and ecological aspects of several sillaginid species have been investigated; notably the coastal shelf species *Sillago sihama* in Indian waters (Radhakrishnan 1957, Reddy & Neelakantan 1992, Hajisamae et al. 2006, Shamsan & Ansari 2010), *S. aenolus* in Japanese waters (Rahman & Tachihara 2005a, b), *Sillaginodes punctata* off southern and south-western Australia (Fowler & Short 1996, Hyndes et al. 1998, Fowler et al. 1999, 2000), and *Sillago analis*, *S. burrus*, *S. vittata*, *S. robusta*, *S. schomburgkii* and *S. bassensis* off western Australia (Coulson et al. 2005, Hyndes & Potter 1996, 1997, Hyndes et al. 1996a,b, 1997). Similarly, the demographic characteristics of the estuarine-nearshore distributed *S. ciliata*, *S. maculata* and *S. analis* have been examined in eastern Australia (Cleland 1947, Burchmore et al. 1988, Kendall & Gray 2009, Stocks et al. 2011). There have been few investigations of the biological characteristics of the eastern Australian coastal shelf species *S. robusta* and *S. flindersi*, even though they are the most abundant sillaginids inhabiting these waters and are subject to substantial (approximately 2000 t per annum) commercial fisheries (Rowling et al. 2010).

The distributions of *S. robusta* and *S. flindersi* overlap off eastern Australia; *S. robusta* consists of 2 disparate populations extending between approximately 24° S and 34° S on the west and east coasts,

whereas *S. flindersi* is endemic to the east and southern mainland coasts as well as around northeastern Tasmania, occurring between approximately 25° S and 44° S (Fig. 1). Both species are an important by-product in coastal penaeid trawl fisheries (Kennelly et al. 1998, Macbeth et al. 2012), whilst *S. robusta* is targeted in a limited entry quota-based trawl fishery in its northern distribution (Butcher & Hagedoorn 2003, Zeller et al. 2012). In contrast, *S. flindersi* is taken across several multi-sector trawl and Danish-seine fisheries managed by different jurisdictions throughout its distribution (Kemp et al. 2012). Depending on the jurisdiction, different input and output controls are used as management tools for each species, including limited entry, fishing gear and vessel restrictions, spatial and temporal closures, legal length limits and total allowable catches. Concerns over discarding in some fisheries have resulted in the development of fishing gears that are more selective at retaining market-sized sillaginids (Broadhurst et al. 2005, Graham et al. 2009). Similar attention to resolving the biological parameters of these species has not taken place. Little is known about important aspects of the reproductive biology of either species, including lengths and ages at maturity, and modes, times and locations of spawning. Without such information, appropriate fishery and species management plans cannot be evaluated.

Previous studies show that sillaginids generally attain sexual maturity at young ages (1 to 3 yr), spawn multiple times over protracted spawning seasons,

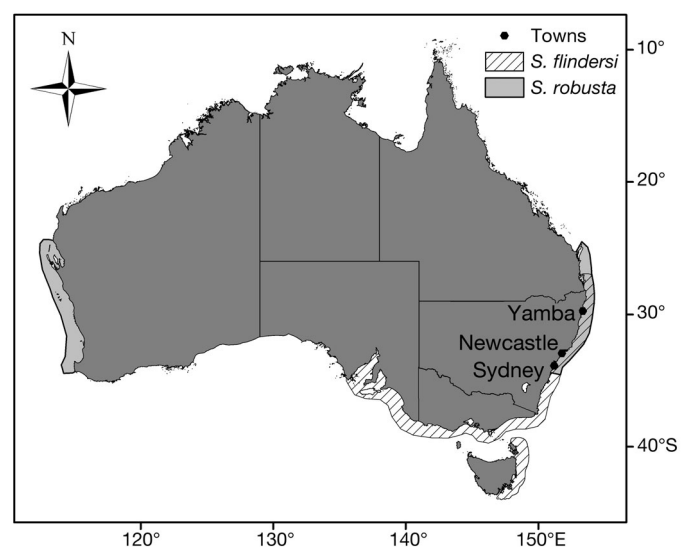


Fig. 1. Distribution of *Sillago robusta* and *S. flindersi* throughout Australia and the Yamba and Newcastle sampling locations off eastern Australia

and display depth-associated ontogenetic shifts in distribution that may assist partitioning of resources (Burchmore et al. 1988, Hyndes et al. 1996a,b, 1997, Kendall & Gray 2009). Here we investigate whether this general paradigm is applicable to *S. robusta* and *S. flindersi* where their distributions overlap in coastal waters off eastern Australia. We specifically test whether the relative abundances, length compositions and reproductive characteristics of populations of these species differ temporally, and between depths and locations.

MATERIALS AND METHODS

Study area and sampling procedures

Sampling was conducted in inner-continental shelf waters (<100 m depth) across transects adjacent to Yamba (29° 26' S, 153° 20' E) and Newcastle (32° 55' S, 151° 45' E) off eastern Australia (Fig. 1). This region is characterised by a dynamic oceanography dominated by the southward flowing East Australian Current and associated eddies (Huyer et al. 1988, Roughan & Middleton 2004, Suthers et al. 2011). The water column is usually thermally stratified in summer but not always in winter, with surface water temperatures typically oscillating between a mean maximum of 24 to 26° C in late summer (February–March) to a mean maximum of 13 to 15° C in late winter/spring (August–September).

Sampling at both locations was stratified across 3 depth ranges; 15–30 m, 31–60 m and 61–90 m; hereafter referred to as the shallow, mid and deep strata respectively. The middle of each depth range corresponded to a distance of approximately 3, 13 and 26 km offshore at Yamba and 1, 7 and 10 km at Newcastle. All sampling was done over soft substrata where commercial trawling for penaeid prawns and whiting regularly occurs. Sampling took place at night within 1 week of the full moon, every 4 weeks at both locations. Sampling extended for 2 full years between November 2005 and November 2007 at Yamba and between October 2006 and November 2007 at Newcastle. Samples were collected using a chartered ocean prawn trawl vessel from each port rigged with standard regulated 'triple' gear, in which each of the 3 nets had a headline length of 10.8 m, stretched mesh of 42 mm hung on the diamond throughout the body and cod-end, the latter which had a circumference of 100 meshes. The general selectivity of *S. flindersi* in this penaeid fishing gear configuration is reported in Broadhurst et al. (2005).

Two replicate tows, each of 60 min bottom duration at an average speed of 2.3 knots (a linear distance of approximately 4.2 km) were completed in each depth strata at both locations at each time of sampling. The depth strata first sampled each month was randomly chosen, after which either the deeper or shallower depths were progressively sampled due to logistic considerations. It took approximately 8 h to complete all 6 tows at each location. For each replicate tow (sample), the catch from all 3 nets was combined and sorted, with all sillaginids identified and kept separate for biological sampling. The number and total weight of each sillaginid species captured in each sample was determined on-board the vessel.

Processing of samples

Whole catches or random sub-samples (100 to 200 individuals) of both species from each replicate tow were counted and measured (fork length [FL] nearest 1 mm) for relative abundance and length composition. The total weight of the catch and subsample were weighed (nearest 5 g). A further subsample of 30 individuals of each species from each replicate tow at each depth was retained on ice for processing in the laboratory. These fish were measured for FL, weighed (wet weight, nearest 0.1 g) and had their gonads removed and weighed (blotted dry weight, nearest 0.1 g) to calculate the gonadosomatic index (GSI) for each individual: $GSI = (\text{gonad weight} / \text{whole fish weight}) \times 100$. Each gonad was staged macroscopically following a development criteria based on oocyte size, colour and visibility adapted from Scott & Pankhurst (1992): for males: I = immature, II = spermatogenic, III = partially spermiated, IV = fully spermiated, V = spent; for females: I = immature, II = immature/regressed, III = vitellogenic, IV = hydrated, V = ovulated, VI = spent. The gonads from a subset of females of both species were kept (preserved in 70 % alcohol) to determine oocyte development and estimate potential batch fecundity (described below in 'Batch fecundity').

Distributions and population structure

General linear models (GLMs), assuming a Gaussian distribution with a log-transformed response variable, were used to test for differences in the relative abundance of each species across depths, seasons nested in years and years at Yamba, and across depths and seasons at Newcas-

tle. Seasons were defined as summer (December–February), autumn (March–May), winter (June–August), spring (September–November) (allowing 2 full years between December 2005 and November 2007). Akaike information criteria (AIC) values were used to determine the most parsimonious model and probability tests (F -tests at $\alpha = 0.05$) were used to determine the influence of each term in each model by comparing change in deviance when each term was included or excluded from the model (Nelder & Wedderburn 1972, Quinn & Keough 2002). Tukey's post-hoc tests ($\alpha = 0.05$) were used to compare the different levels of each significant factor. Differences between depths in the length compositions of each species (pooled across seasons) at each location were tested using Kolmogorov-Smirnov (K-S) tests.

Oocyte development

Histological examination of a selection of preserved (70 % alcohol) Stage II, III and IV ovaries of both species was used to determine the development pattern of oocytes and to verify the macroscopic staging of females. Small sections were dissected from the middle of each ovary, treated in an automated tissue processor, with the resulting tissues embedded in paraffin wax and sectioned at 5 μm thickness on a rotary microtome. Sections were deparaffinised, differentiated in acidified alcohol and stained in alcoholic eosin. Histological staging was based on the most advanced cohort of oocytes in each ovary section (West 1990).

Individual oocyte development was examined by determining the size distributions of oocytes in 10 random individuals of each species with Stage III ovaries. The entire ovary was blotted dry and weighed (0.0001 g), after which 3 replicate sub-samples were taken from the mid-section of each ovary, blotted dry, weighed (0.0001 g) and placed in a sealed 70 ml sample jar containing 70 % alcohol solution. Each sub-sample was placed in a sonic bath (Unisonics FXP4) for a period no longer than 20 min to dislodge individual oocytes from surrounding connective tissue (Barnes et al. 2013). Oocytes from each sub-sample were transferred into a petri-dish, separated from each other, scanned and imaged at 1200 dpi resolution. Image analysis software (Image J, Version 1.38) was used to determine the number and size of oocytes in each sub-sample. Size-frequency plots of oocyte diameters were produced for each gonad.

Length at maturity

The estimated FL at which 50 % (L_{50}) of males and females attained reproductive maturity was determined by fitting a logistic regression model using the binomial GLM function in R to the proportions of immature (Stages I and II) and mature (Stages III and above) fish in each 1 mm length class. The data used in these analyses was obtained during periods of high GSI. Differences between sexes and locations (and years for Yamba) in the estimated L_{50} values of each species were tested using the 2-sampled Z technique with $\alpha = 0.05$ (Gunderson 1977).

Reproductive period

Temporal changes in mean male and female GSI values and proportions of fish with each macroscopic gonad stage (of individuals larger than the estimated mean length at maturity) were used to estimate the timing of spawning. Elevated GSI values and high proportions of fish with gonads staged III to VI were interpreted as probable spawning. The GLM procedures outlined above ('Distributions and population structure') were used to examine the influence of depths, seasons and, where relevant, year and seasons nested in year, on the proportions of mature individuals of each species present at each location. These GLMs assumed a binomial distribution, treating maturity as a binary response variable (1 = mature and 0 = immature), and used chi-squared ($\alpha = 0.05$) probability tests within the analysis of deviance tables.

Batch fecundity

The largest size class of oocytes (vitellogenic, >0.30 mm for *S. robusta* and >0.35 mm for *S. flindersi*) in mature, pre-spawning (Stage III) fishes were considered suitable for estimating potential batch fecundity (BF) (Hunter et al. 1985). The ovaries of up to 25 individuals from each species collected mid-spawning season at each location and in both years were examined. For each individual, the number of oocytes present was calculated using the same methodologies describe above ('Oocyte development') for investigating oocyte size–frequency distributions. Potential BF was estimated by scaling the number of oocytes present within the weighed ovarian subsample to the total preserved weight of the ovary. Log-linear models were used to describe relationships between estimated BF and FL and ANCOVA were used to test

whether BF for each species differed according to location and FL.

RESULTS

Relative abundance

The GLMs showed that depth and season influenced the relative abundance of *Sillago robusta* and *S. flindersi* in different ways. Notably, *S. robusta* were most abundant in the shallow strata across most seasons at Yamba and Newcastle (Tukey's HSD tests: $p < 0.05$, Fig. 2), whereas, *S. flindersi* were consistently most abundant in the mid-depth strata across all seasons at Yamba (for which data were combined across years) and at Newcastle (Tukey's HSD tests:

$p < 0.05$, Fig. 2). Neither species was consistently caught in large numbers in the deep strata, with *S. robusta* only found deep in spring, and *S. flindersi* only in spring and winter at Yamba.

Seasonal changes in the relative abundance of each species at each location were inconsistent and dependent on depth and year (where relevant). For example, abundances of *S. robusta* at Yamba (data combined across depths) did not show any significant differences between seasons in 2006, whereas they were significantly greater in summer and autumn in 2007 (Tukey's HSD tests: $p < 0.05$, Fig. 2). At Newcastle, abundances of this species only varied between seasons in the shallow strata, where they were significantly greater in summer compared to winter (Tukey's HSD test: $p < 0.05$, Fig. 2). In contrast, abundances of *S. flindersi* at Yamba (data combined across years and depths) were greatest in winter and spring (Tukey's HSD test: $p < 0.05$, Fig. 2), whereas at Newcastle they were significantly lowest in autumn (Tukey's HSD test: $p < 0.05$, Fig. 2).

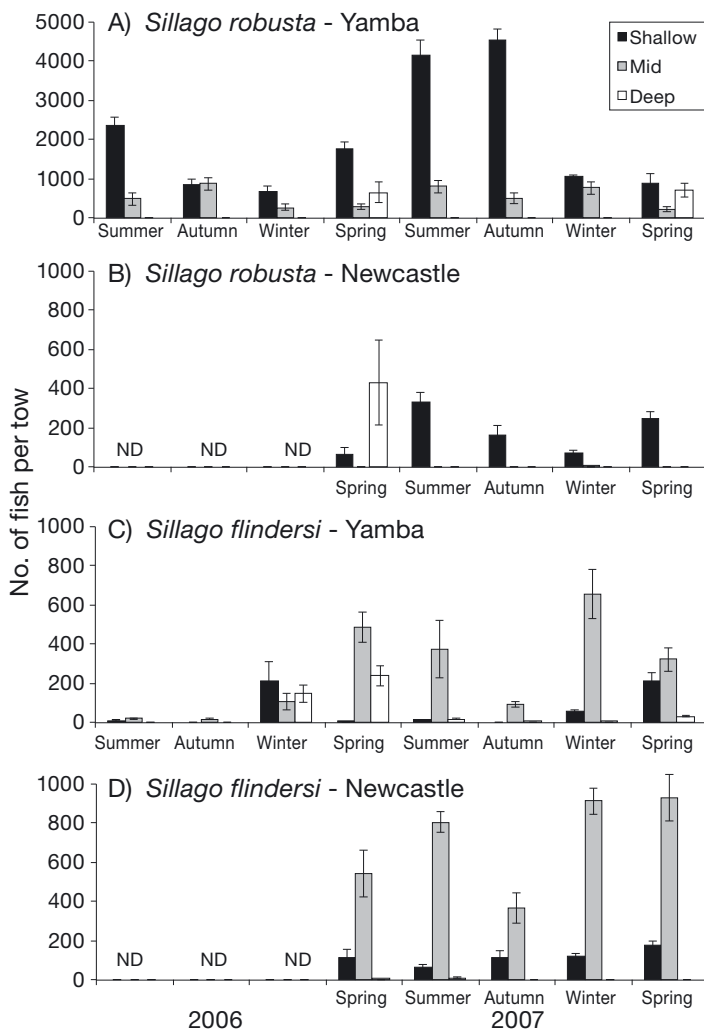


Fig. 2. Mean (\pm SE) number of *Sillago robusta* and *S. flindersi* caught per tow in the shallow, mid and deep depth strata in each season at Yamba and Newcastle. ND: no data

Population structure

The length compositions of samples of each species differed significantly according to depth and location (multiple K-S tests, $p < 0.05$ in all cases). Despite this, some general patterns were evident; notably a similar length range of *S. robusta* was present across all depth strata within each year at Yamba, and in the shallow and deep strata at Newcastle (Fig. 3). A cohort of small-sized (< 10 cm FL) *S. robusta* was present in the shallow and mid-depth at Yamba in 2006 but not in 2007. For *S. flindersi*, a cohort of smaller-sized (< 13 cm FL) individuals predominated the shallow strata at both locations, whereas the mid and deep strata primarily contained individuals > 13 cm FL (Fig. 3). This later length cohort was also prominent in the shallow strata at Yamba in 2007.

Oocyte development

Both species displayed a similar pattern of ovarian development. Stage II ovaries contained unyolked oocytes of a variety of sizes, whereas Stage III ovaries contained a mixture of unyolked oocytes, partially yolked oocytes and oocytes that were in an advanced yolk stage of development (Fig. 4). The diameter sizes of this latter cohort of oocytes ranged from 0.30 to 0.45 mm for *S. robusta* and 0.35 to 0.50 mm for *S. flindersi* (Fig. 5). This suggested that *S. flindersi*

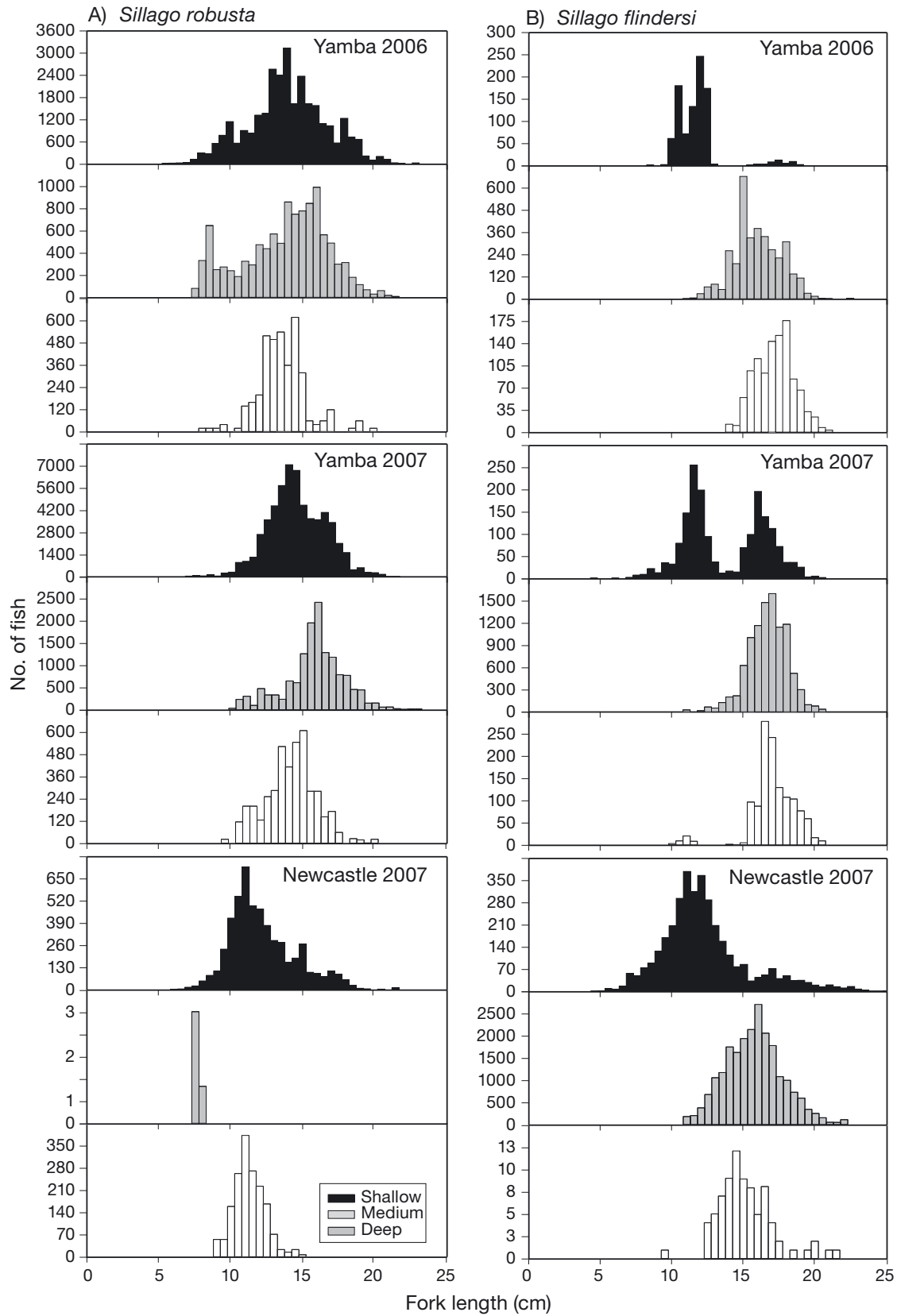


Fig. 3. Population length composition of *Sillago robusta* and *S. flindersi* in the shallow, mid and deep depth strata at Yamba and Newcastle. Data pooled across all sampling times for each year. Note different scales of y-axes

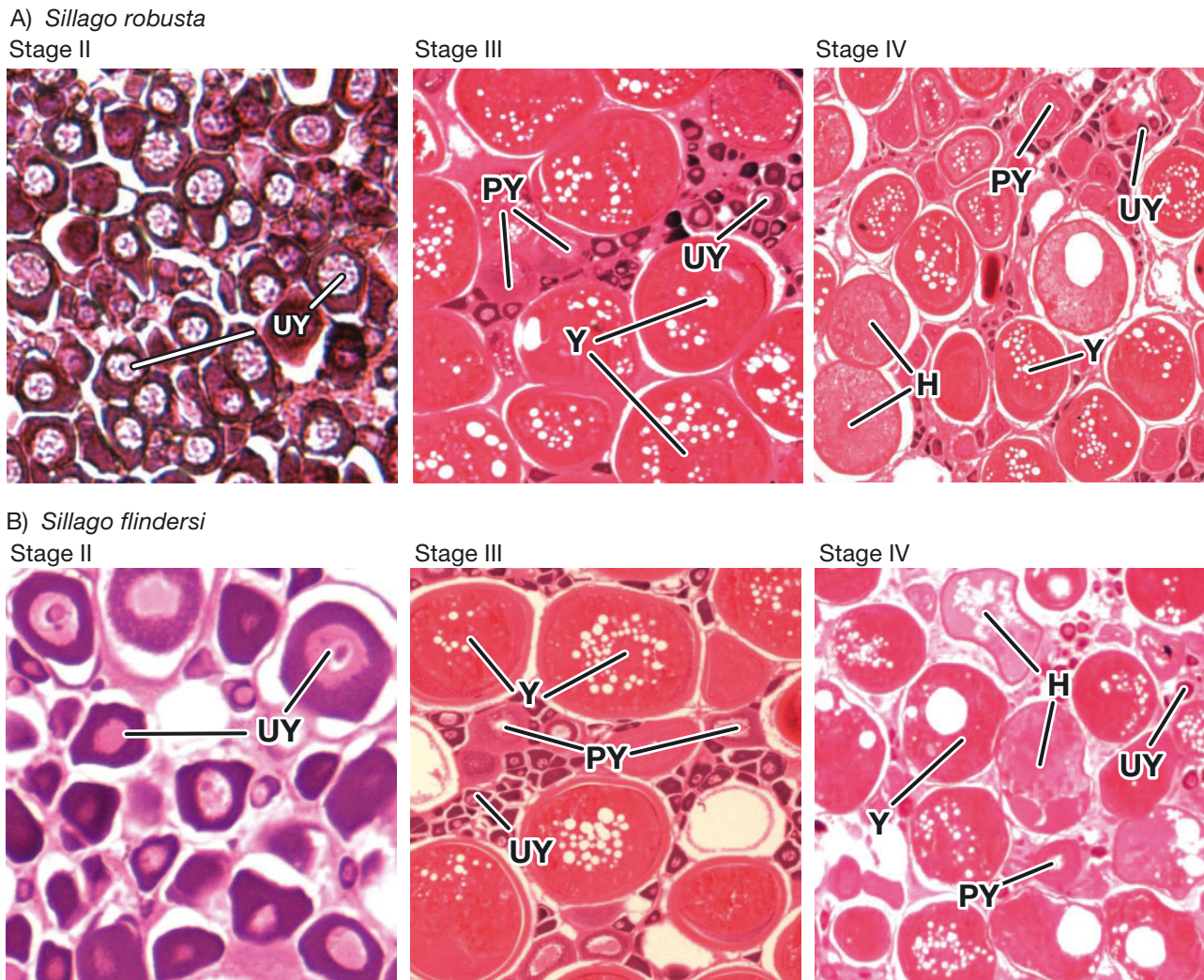


Fig. 4. Photos showing microscopic characteristics of ovary stages II, III and IV for *Sillago robusta* and *S. flindersi*. Stage II: immature ovary containing developing unyolked (UY) oocytes, Stage III: mature ovary containing unyolked oocytes, partially yolked (PY) oocytes and advanced yolk (Y) stage oocytes, Stage IV: mature ovary containing oocytes in all other stages of development as well as hydrated (H) oocytes

might have produced larger eggs than *S. robusta*. Stage IV ovaries contained hydrated oocytes as well as oocytes in each of the previous stages of development (Fig. 4).

Length at maturity

There was no consistent effect of sex on length at maturity for either species. Notably, the L_{50} was significantly ($p < 0.05$) smaller for males than females of both species at both locations in 2007, but this was not the case in 2006 when the L_{50} was significantly ($p < 0.05$) greater for male than for female *S. robusta* and there was no significant ($p > 0.05$) difference between sexes for *S. flindersi* (Fig. 6). Evidence of

spatial interactions in length at maturity was also apparent, with the L_{50} of *S. robusta* being significantly ($p < 0.05$) smaller at Newcastle for both sexes (Fig. 6). Significant spatial difference of length at maturity was also observed for female *S. flindersi*, which was greatest at Newcastle ($p < 0.05$), but not for males ($p > 0.05$). Males displayed temporal variations, with the L_{50} being significantly ($p < 0.05$) larger for both species at Yamba in 2006.

The estimated L_{50} values for male and female *S. robusta* ranged from 12.84 to 15.35 cm FL and from 14.08 to 14.83 cm FL, respectively (Fig. 6). Similarly, the estimated L_{50} values for male and female *S. flindersi* ranged from 13.27 to 13.96 cm FL and from 13.88 to 14.87 cm FL, respectively. The observed smallest mature male and female *S. robusta* was 11.3 and

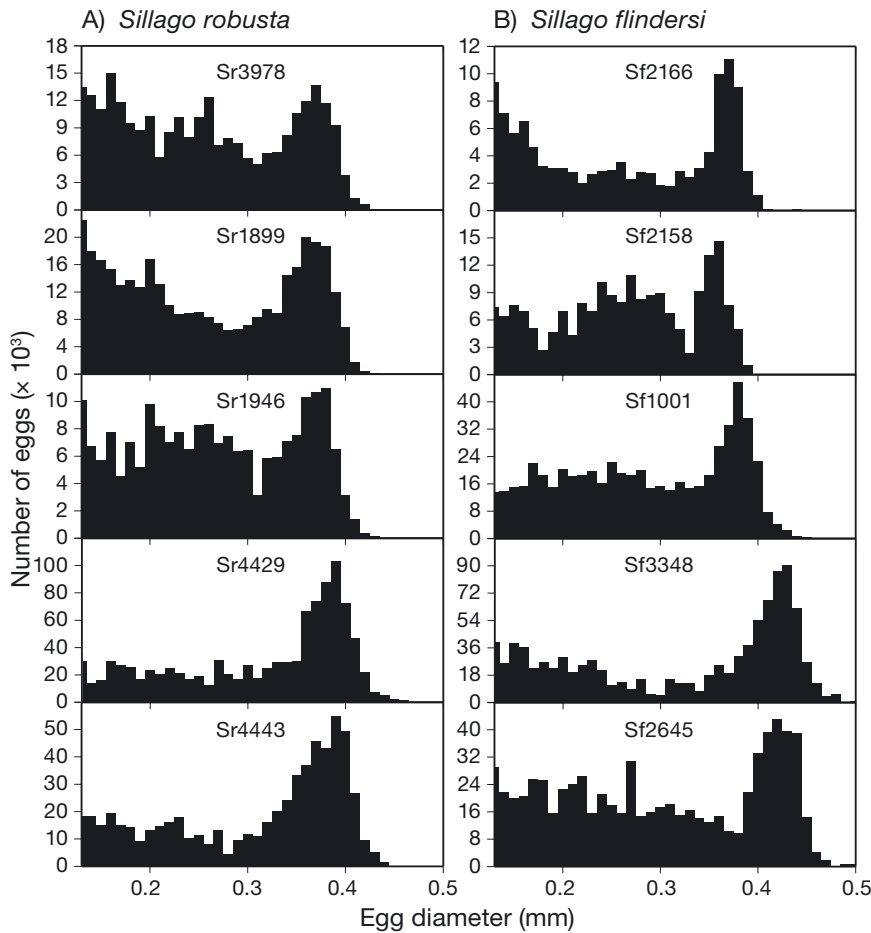


Fig. 5. Size distributions of oocytes in 5 individual Stage IV ovaries of *Sillago robusta* and *S. flindersi*. Numeric code refers to individual sample. Note different scales of y-axes

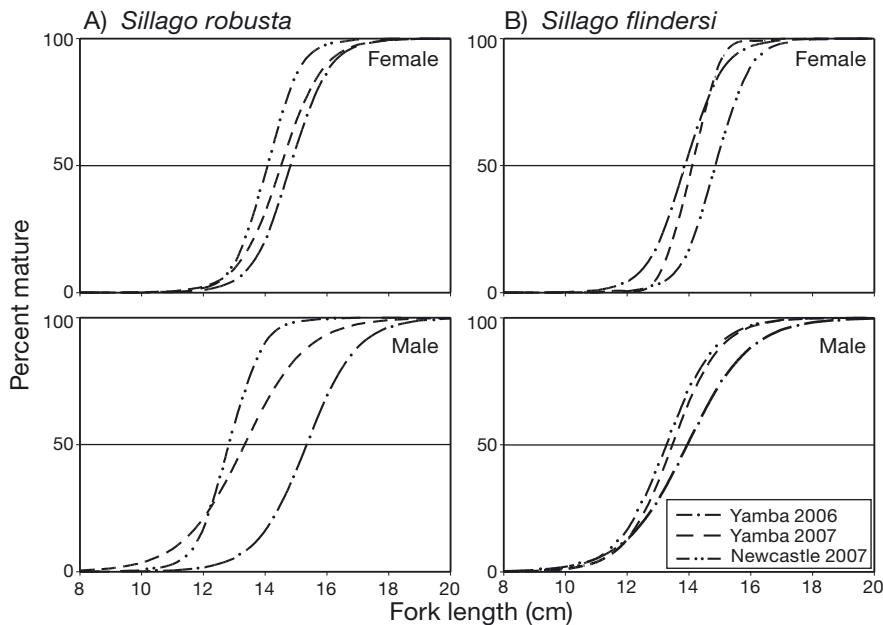


Fig. 6. Estimated maturity ogives of female and male *Sillago robusta* and *S. flindersi* at Yamba and Newcastle. Data combined across depth strata

13.0 cm FL at Yamba and 11.4 and 12.5 cm FL at Newcastle, respectively. Likewise, the observed smallest mature male and female *S. flindersi* was 11.1 and 11.6 cm FL at Yamba and 11.0 and 13.0 cm FL at Newcastle, respectively.

Spawning

The macroscopic staging of gonads and changes in mean GSI values indicated both species potentially spawned year-round at both locations. Female and male *S. robusta* and *S. flindersi* with mature gonads (Stage III and higher) were present each month at Yamba (except June 2007 for *S. flindersi*) and most months at Newcastle (Fig. 7). Further, for both species ovaries containing hydrated eggs (Stage IV) were collected across most months at Yamba, although few were observed at Newcastle. There was also no consistent pattern for either species as to the months when particular gonad stages (mature/immature) were most or least prevalent. Nevertheless, for *S. robusta* a greater proportion of Stage I individuals were present in 2006 than 2007 at Yamba (Fig. 7)

The mean GSI values of female and male *S. robusta* at Yamba displayed similar trends through time and were generally lowest in late autumn and winter (April to July in 2006 and May to July in 2007). Mean GSI values tended to be highest between September and March in both years, suggesting that potentially a greater proportion of individuals spawn throughout the austral spring and summer (Fig. 8). There was no evidence of any such trend for this species at Newcastle where mean GSI values were relatively high between April and October. The maximum mean (\pm SE) monthly GSI for female and male *S. robusta* was 2.86 ± 0.12 and 2.55 ± 0.23 at Yamba and 3.27 ± 0.82 and 1.85 ± 0.19 at New-

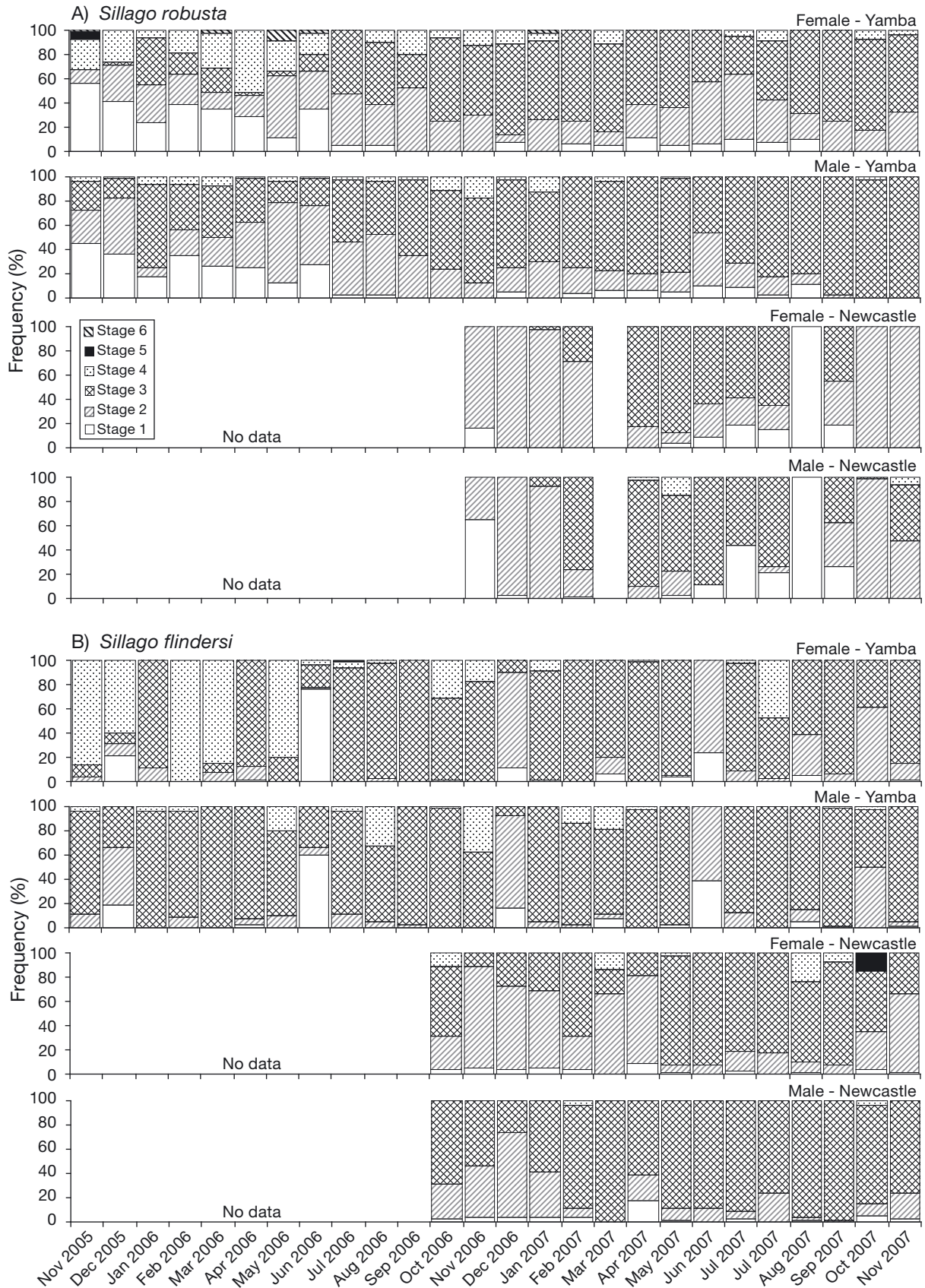


Fig. 7. Frequency of different macroscopically staged ovaries and testis of *Sillago robusta* and *S. flindersi* at Yamba and Newcastle. Data combined across depth strata

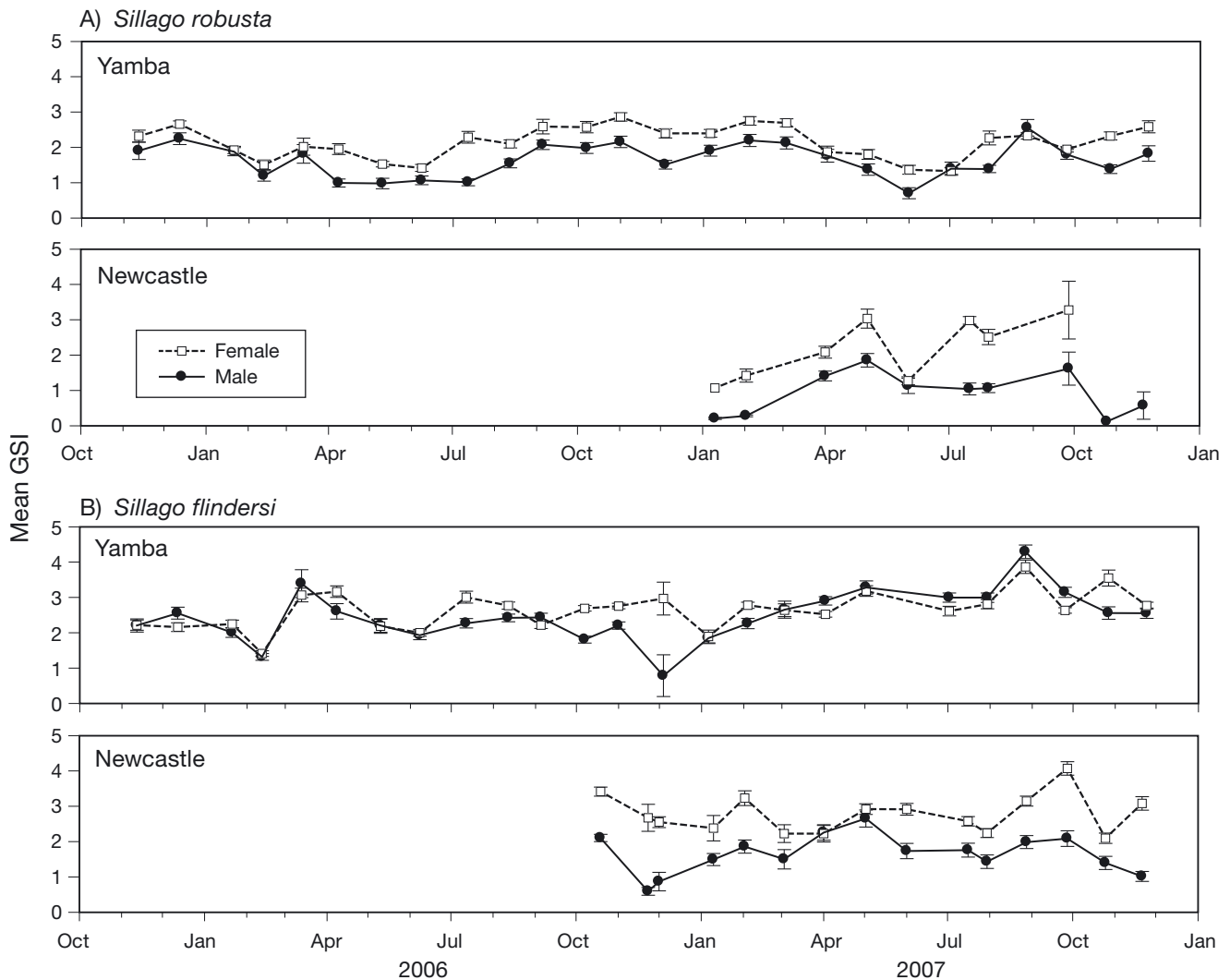


Fig. 8. Monthly variation in mean (\pm SE) GSI of female and male *Sillago robusta* and *S. flindersi* at Yamba and Newcastle. Data combined across depth strata

castle, respectively. The mean GSI values of male and female *S. flindersi* remained relatively stable, displaying no seasonality throughout sampling at either location (Fig. 8). The maximum mean (\pm SE) monthly GSI for female (male) *S. flindersi* was 3.87 ± 0.18 and 4.29 ± 0.19 at Yamba and 4.07 ± 0.19 and 2.65 ± 0.24 at Newcastle, respectively.

For both species, the effect of year could not be tested due to significant depth \times season (nested in year) and depth \times year interactions. The maturity data collected from Yamba were therefore analysed in separate GLMs for the 2 years. The GLMs identified that a greater proportion of mature *S. robusta* occurred in the mid compared to the shallow strata in summer, winter and spring of 2006 and in summer, autumn and spring of 2007 at Yamba (Tukey's HSD test: $p < 0.05$, Fig. 9; note that, for both years, this species was only caught in the deep strata dur-

ing spring). In contrast, the significant depth-related effect in the GLM reflected a predominance of mature fish in the shallow strata compared to the deep strata at Newcastle (GLM: $p (>Chi) < 0.05$, Fig. 9; but note that this species was primarily only caught in the shallow strata and very few were caught in the mid strata irrespective of season). A significantly greater proportion of mature *S. flindersi* occurred in the mid and deep strata compared to the shallow strata across most seasons in both years at Yamba (Tukey's HSD test: $p < 0.05$, Fig. 9). At Newcastle, the greatest proportion of mature *S. flindersi* occurred in the mid strata in winter and autumn (Tukey's HSD test: $p < 0.05$, Fig. 9; note that no *S. flindersi* were captured in the deep strata during these seasons) but in the deep strata in spring 2006 and summer 2007 (Tukey's HSD test: $p < 0.05$, Fig. 9).

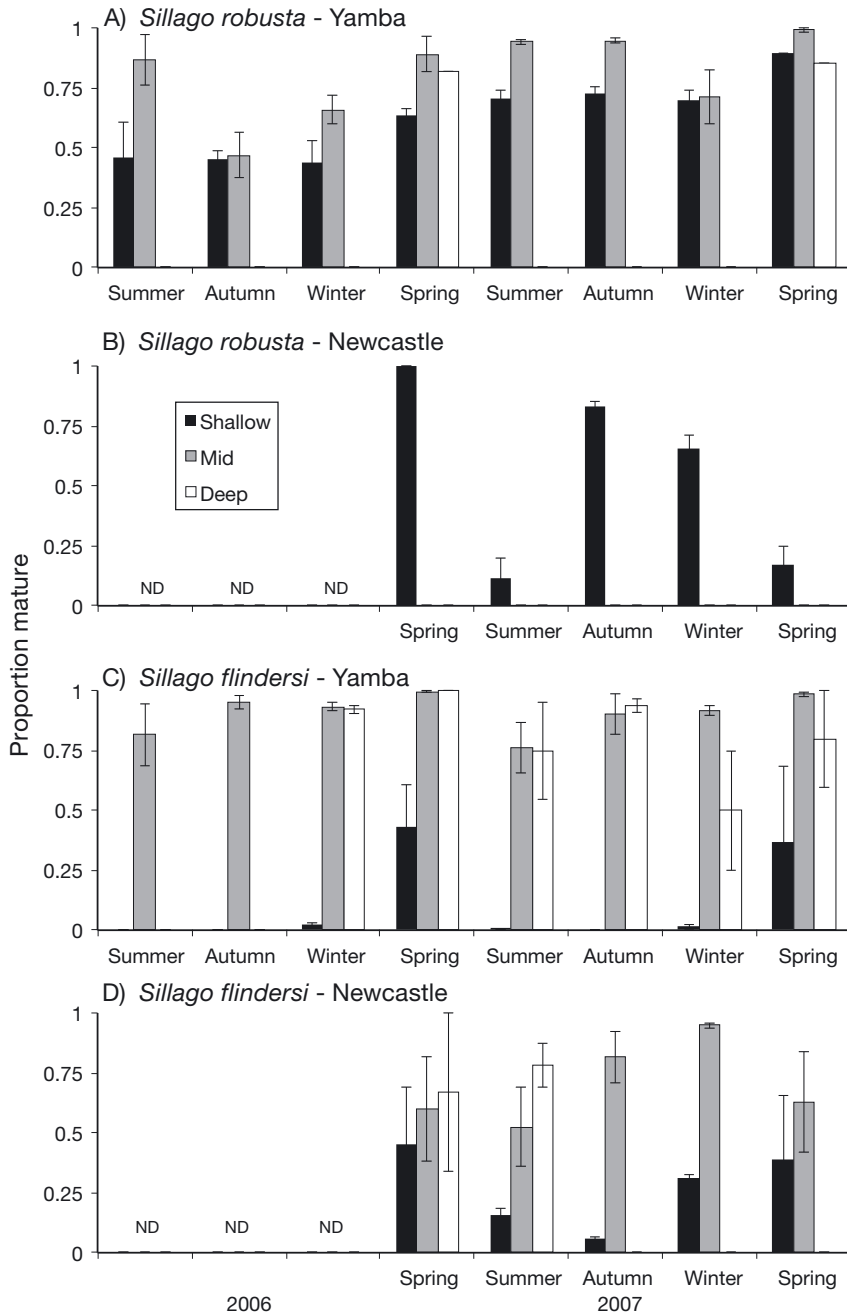


Fig. 9. Mean (\pm SE) proportion of mature *Sillago robusta* and *S. flindersi* in the shallow, mid and deep depth strata in each season at Yamba and Newcastle. ND: no data

Batch fecundity

There was no significant difference between locations in the relationship between estimated BF and FL for either species (ANCOVA, $p > 0.05$ in all cases), so data were combined across locations for each species. Estimated BF of both species significantly increased with FL ($p < 0.001$ in both cases); the log-linear rela-

tionship [$\log(\text{BF}) = \log(a) + b \times \log(\text{FL})$] was: $\log(a) = -3.0787$, $b = 4.9280$, $r^2 = 0.6921$, $n = 25$ for *S. robusta* and $\log(a) = -5.2534$, $b = 5.5159$, $r^2 = 0.7524$, $n = 24$ for *S. flindersi*. Estimated BF ranged from 7048 to 284 755 eggs for *S. robusta* measuring 13.0 to 21.6 cm FL, and from 6773 to 256 100 for *S. flindersi* measuring 13.1 to 23.4 cm FL. These data indicated that at a given FL, fecundity was greater in *S. robusta* than in *S. flindersi*.

DISCUSSION

Population structuring and habitat partitioning

Spatial and temporal structuring of eastern populations of *Sillago robusta* and *S. flindersi* was evident along a number of gradients suggesting possible partitioning of resources similar to other sympatric Sillaginidae (Hyndes et al. 1996a,b, 1997) and teleost families (Ross 1977, Genner et al. 1999, Barnes et al. in press). In general, *S. robusta* was more prevalent in the shallow strata whereas *S. flindersi* mostly occurred in the mid strata, while neither species consistently utilised the deep strata. Depth stratification of sillaginid and teleost populations and assemblages is widespread (Werner et al. 1977, Hyndes et al. 1999, Labropoulou et al. 2008, Gray et al. 2011).

The population length structure of *S. robusta* was similar across all depth strata, which is concordant with western populations of the species (Hyndes & Potter 1996). In contrast, smaller and immature *S. flindersi* were more prominent in the shallow strata compared to the mid and deep strata, which were dominated by larger (mature) individuals. These data support the 'smaller-shallower' phenomena (Middleton & Musick 1986, Stefanescu et al. 1992) and suggest that *S. flindersi* uses the shallow strata as a nursery area and then moves to deeper waters with growth and maturity. This is synonymous with the hypothesised life history of other Sillaginidae, including coastal *S. bassensis* and *S. vittata* (Hyndes & Potter 1996, Hyndes et al. 1996b) and estuarine *S. ciliata* and *S. maculata* (Weng 1986,

Burchmore et al. 1988). Depth-related ontogenetic shifts in distribution are common among teleosts (Macpherson & Duarte 1991, Methratta & Link 2007, Labropoulou et al. 2008), with shallow waters hypothesised to provide more food and greater protection of juveniles from predators (Ryer et al. 2010). Such stratification is also a potential mechanism to reduce intra- and interspecific competition and aid broad-scale partitioning of resources among co-occurring species (Hyndes & Potter 1996, 1997). In the present study, the shallow-water preference of small *S. flindersi* placed them directly in the preferred habitat of *S. robusta*. It is conceivable that a dietary mechanism ensured the smaller *S. flindersi* individuals were not competitively disadvantaged (Hyndes et al. 1997, Barnes et al. 2011). Alternatively, necessary resources in the shallow strata may not have been limited, reducing the need for species stratification.

Spawning

The data presented here indicate that *S. robusta* and *S. flindersi* are income-spawners (McBride et al. 2013), yet each species may have evolved slightly different reproductive strategies to deal with the dynamic coastal environment they inhabit. Despite neither species investing greatly in reproduction (low GSI values of females and males), the larger-growing *S. flindersi* generally displayed higher GSI ratios, suggesting it invests more energy into gonad production than *S. robusta*. Comparable differences in reproductive investment between other co-occurring Sillaginidae have been observed (Hyndes & Potter 1996). Further, our data suggest that *S. flindersi* produced fewer (at any given length) but potentially larger eggs than *S. robusta*. We could not ascertain here, however, the effects of such trade-offs between the potential quality and quantity of larvae produced (Duarte & Alcaraz 1989) on the reproductive success and population replenishment of either species.

Despite these apparent differences, the ovaries of mature *S. robusta* and *S. flindersi* contained oocytes of multiple sizes and developmental stages, indicating their potential to spawn several times within a given 'spawning' period (De Vlaming 1983, Hunter & Macewicz 1985, West 1990). This concurs with other sillaginids (Lee & Hirano 1985, Hyndes & Potter 1996, Fowler et al. 1999, Kendall & Gray 2009), adding further support to the hypothesis that the Sillaginidae are multiple-batch spawners. This spawning strategy is widespread among teleosts (Sarre & Potter 1999, Walsh et al. 2011, Gray et al. 2012), allowing individuals

to maximize the number of eggs produced over a particular period (Burt et al. 1988, McBride et al. 2013).

Mature individuals of both species could potentially spawn over extended periods. Fowler et al. (1999) estimated that individual *Sillaginodes punctata* spawned at least 20 times throughout their 3 mo spawning period. We could not determine the frequency and number of times an individual of either species may have released eggs throughout any given period or throughout its life. Consequently, the total number of eggs that each individual produces each year (total fecundity) could not be estimated. Nevertheless, estimated batch fecundity in both species was positively related to fish length, indicating that reproductive output is potentially greater in larger individuals, as in most teleosts (Parker 1992). Having a greater abundance of larger (and presumably older) individuals could theoretically increase the collective reproductive potential of teleost populations, and enhance larval survival (Berkeley et al. 2004). Fishing gears that allow a greater proportion of fish to reach larger sizes could enhance the reproductive potential and sustainability of these sillaginid populations.

The potential year-round spawning of *S. robusta* and *S. flindersi*, as evidenced by changes in GSI values and the macro- and microscopic staging of gonads, is further corroborated by the occurrence of pelagic larvae of both species year-round in coastal waters off eastern Australia (Gray & Miskiewicz 2000). This extended period of spawning is in contrast to western populations of *S. robusta* occurring at similar latitudes that spawn between December and March (Hyndes & Potter 1996). Our data indicate, however, that a greater proportion of the eastern populations of *S. robusta* spawn between September and March. This predominate spring–summer spawning pattern is also true for the east-Australian estuarine-based sillaginids *S. ciliatia* and *S. maculata* (Morton 1985, Burchmore et al. 1988, Kendall & Gray 2009) as well as a suite of other coastal sillaginids, including *S. burrus*, *S. bassensis*, *S. schomburgkii*, *S. vittata* and *S. aeolus* (Hyndes & Potter 1996, 1997, Hyndes et al. 1996b, Rahman & Tachihara 2005a). Periods of increasing water temperature and photoperiod may potentially trigger reproductive development and spawning in these species (Hyndes & Potter 1996). In contrast, similar proportions of the *S. flindersi* populations sampled here spawned year-round, indicating that changes in water temperature and photoperiod were not the primary cue to trigger reproductive development and spawning in this species.

The extended spawning of eastern populations of *S. robusta* and *S. flindersi* and the potential ability of

individuals to spawn multiple times in a spawning season is probably an adaptation to the stochastic and dynamic oceanography of this coastal region. This strategy should enhance the probability of successful survival and recruitment of some eggs and larvae (Lambert & Ware 1984, Lowerre-Barbieri et al. 2011, McBride et al. 2013) and could also be a life history tactic to enhance dispersal of young as well as maintaining genetic connectivity among populations along eastern Australia, as suggested for other coastal boundary current inhabitants (Hare & Cowen 1993, Gray et al. 2012). Further, spawning by species in the depths examined here may be advantageous to maximising alongshore dispersal and subsequent retention of eggs and larvae in shelf waters by the East Australian Current (Roughan et al. 2011).

The observed prolonged reproductive period of both species in eastern Australia compared to other sillaginid populations could also potentially be a response to high levels of fishing-related mortalities in these particular populations. High exploitation rates can impact teleost reproductive strategies, including lowering sizes and ages at maturity, increasing egg production and spawning frequency, and lengthening spawning periods (Rochet 1998, Sharpe & Hendry 2009, Wright & Trippel 2009). The sillaginid populations examined here have been commercially harvested for over 100 yr, with catches over the past 20 yr exceeding 2000 t per annum. These levels of exploitation could potentially be sufficient to have already caused modifications of reproductive strategies of these populations.

Despite the differences outlined above, spawning of *S. robusta* and *S. flindersi* overlapped greatly in space and time. This is common among closely related teleosts (Muthiga 2003, Park et al. 2006, Tomauiolo et al. 2007) and may be related to similar evolutionary histories and environmental requirements (Mercier & Hamel 2010). Thus, there was no specific evidence of large-scale reproductive isolation between these sillaginid species (Wellenreuther & Clements 2007). Reproductive isolation can occur between sympatric species over much finer spatial and temporal scales than examined here (Colin & Clavijo 1988, Colin & Bell 1991, Sancho et al. 2000), which could be further explored in these species.

Maturity and fishery considerations

The estimated L_{50} for both species were mostly smaller for males compared to females, which is in general agreement with other sillaginids (Kendall &

Gray 2009). Length at maturity of *S. robusta* as determined here was greater by about 1.5 to 2.0 cm than for western populations (Hyndes & Potter 1996). A plethora of biotic and abiotic factors, as well as anthropogenic influences (e.g. fishing) can potentially cause broad-scale variations in length (and age) at maturity among populations (Lassalle et al. 2008). Importantly, these data demonstrate the potential for intraspecific plasticity in life history characteristics among discrete populations of teleosts (Gust et al. 2002, Ruttenberg et al. 2005, Blanck & Lamouroux 2007, Sala-Bozano & Mariani 2011), emphasising the need for regional information of population demographics for fisheries assessment and management.

Significant spatial and temporal differences in the estimated L_{50} of each species were also detected at the smaller regional scale examined here, with differences in parameter estimates between years being equal to between locations. Although such results could be artefacts of variations in sample composition, they demonstrate the potential limitations of such demographic information collected at one place and time (i.e. typical snapshot studies). Indeed, a lack of information of levels of variability in demographic parameters (including rates of growth and mortality) across a species distribution could confound biological-based fisheries assessments and management plans (Morgan & Bowering 1997, Ruttenberg et al. 2005, Jakobsen et al. 2009).

Fisheries managers often set the retained legal lengths of fish at the L_{50} to potentially allow 50% of individuals to spawn at least once prior to harvesting (King & McFarlane 2003). Since eastern populations of *S. robusta* and *S. flindersi* are often caught together in large quantities as by-product by commercial trawlers targeting penaeid prawns, a common retained legal length of 14 cm FL (~15 cm total length) could be applied to these species in these fisheries if required. This length corresponds closely to the 50% length selection for these species in 35 mm square mesh cod-ends tested and recommended for use in the east Australian demersal penaeid trawl fisheries in which these species are an important by-product (Broadhurst et al. 2005, Graham et al. 2009, Macbeth et al. 2012). For other fisheries in which these sillaginids are the target species, having gears that specifically select fish $> L_{50}$ (e.g. 20 cm FL) could aid reproductive potential and resource sustainability. In high-volume multispecies trawl fisheries, it is often preferable to manage and regulate the sizes of fish retained by prescribing the selectivity of the fishing gears rather than enforce-

ment of specific legal lengths, which can be logistically problematic for fisheries operators as well as compliance officers. Nevertheless, prior to introducing and mandating any specific fishing gears (or retained legal lengths for these sillaginid species) in any particular fishery, assessments of rates of survival of non-retained individuals in such fishing gears (Broadhurst et al. 2006, Coggins et al. 2007), as well as broader market and economic impacts need to be considered. Moreover, the potential effects on population reproductive output and resource sustainability of alternate management arrangements that protect larger (more fecund) fish, either by harvesting particular slot sizes (Gwinn et al. 2013) or provision of refuge (no-take) areas (Roberts et al. 2005) needs investigating.

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