



## Reproductive biology of largehead hairtail (*Trichiurus lepturus*) in south-eastern Australia

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### ABSTRACT

Knowledge of reproductive biology and life-history traits of populations exploited by fisheries is important for their sustainable management. We investigated the life-history traits of *Trichiurus lepturus* (largehead hairtail) in south-eastern Australia; a region of low exploitation for this otherwise heavily exploited circumglobal species, to investigate whether there were differences in the reproductive biology and life-history traits in the south-east Australian population compared with those in other regions. We also used histological sections to examine male and female gonads at a microscopic level. *Trichiurus lepturus* in south-eastern Australia had a greater maximum length (193 cm total length (TL)), matured at a larger length (108 cm TL at 50% mature) and had a spawning period (March to September, Austral winter) that was inconsistent with other regions. The overall sex ratio of 1:0.4 females: males was consistent with a female dominant sex ratio observed in other regions, particularly in larger length classes. However, females in the current study dominated samples from both estuarine and coastal habitats, as well as during the spawning and non-spawning periods, which is not consistent with the patterns found in other regions. Differences in south-eastern Australia may relate to limited fishing pressure, genetic variation, or differences in environmental factors that influence reproductive development, including temperature, trophic resources and habitat.

### 1. Introduction

Knowledge of reproductive biology and life-history traits, including maximum body length, is important for understanding the productivity of exploited fish stocks and therefore their resilience (Bradford et al., 2014; Jessop, 2010; Lowerre-Barbieri et al., 2017; Randall et al., 2013). Overfishing of large-bodied individuals, for example, may result in selection for maturation at earlier ages and smaller body lengths (Ghosh et al., 2014; Kuparinen & Merilä, 2007). Consequently, studies on the life-history traits of exploited species should consider the unique suite of pressures experienced by individual stocks.

Largehead hairtail (*Trichiurus lepturus*) is a trichiurid species with a broad distribution across the globe. It is subject to intense fishing pressure in numerous regions. The species is reported in all non-polar oceans, with latitudinal distribution extending from temperate waters at 60° N, through equatorial waters to southern temperate waters at 45° S (Al-Nahdi et al., 2009; Carvalho & Luque, 2011; Chiou et al., 2006; FAO, 2018; Shih et al., 2011). *T. lepturus* is highly abundant between 25° N and 35° S (Martins & Haimovici, 1997); however, within this

latitudinal range, there is large variation in fishery landings among countries (De la Cruz-Torres et al., 2014; Wang & Liu, 2013). Excessive fishing pressure has resulted in the over-exploitation of *T. lepturus* stocks in some regions, with reports of localised depletions from China (Zhang et al., 2018), India (Ghosh et al., 2009), Japan (Watari et al., 2017) and Korea (Kim et al., 2005).

Reported life-history traits of *T. lepturus* suggest the species is relatively productive; however, there are variations among regions (James et al., 1978; Kwok & Ni, 1999; Lazarus & Sarma, 1991; Martins & Haimovici, 2000; Sheridan et al., 1984; Tampi et al., 1968; Thiagarajan et al., 1992; Wojciechowski, 1972). Investigations have generally found that *T. lepturus* is relatively short-lived, fast-growing (Del Toro, 2001) and is a multiple batch spawner (Al-Nahdi et al., 2009; Del Toro, 2001; Ghosh et al., 2014; Khan, 2006; Kwok & Ni, 1999; Martins & Haimovici, 2000) with a prolonged spawning period (Ghosh et al., 2009; Khan, 2006; Ye & Rosenberg, 1991). Sex ratio of *T. lepturus* across regions are generally skewed toward females, especially in larger length classes (Del Toro, 2001; Reuben et al., 1997). Defined spawning periods (from spring to summer) have been found at higher latitudes like the Sea of Japan

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(Munekiyo & Kuwahara, 1984) and the South Atlantic Ocean off south-eastern Brazil (Bellini, 1980), while flexible spawning periods were observed at lower latitudes like the Arabian Sea off south-western India (James et al., 1978; Lazarus & Sarma, 1991) and south-eastern India (Narasimham, 1972; Tampi et al., 1968). Given the geographical variation reported in reproductive biology, regional-specific information is likely required to inform sustainable fisheries management.

Commercial landings of *T. lepturus* in Australia are low compared to other regions of the world (Stewart et al., 2015). Most landings are taken from the south-eastern state of New South Wales (NSW), where the species is caught by both the commercial and recreational sectors (Stewart et al., 2015). The average annual commercial fishery landings are approximately 35t, with annual landings peaking at 160 t, which is much lower than landings in other regions (e.g. 910 000 t in China (Wang & Liu, 2013)). An estimate of recreational catch from south-eastern Australia is not available, but it is an important species for the recreational sector (Stewart et al., 2015). NSW provides an opportunity to examine reproductive characteristics of *T. lepturus* under relatively low fishing pressure, providing a contrast to similar studies elsewhere.

No reproductive information is available for *T. lepturus* in south-eastern Australia. Our objective in this study was to determine the maximum length, length at maturity, spawning period and the spatial and temporal patterns of sex ratio for *T. lepturus* along the south-eastern coast of Australia. Findings from this study will inform development of management measures that maintain adequate reproductive potential within the population.

## 2. Materials and methods

### 2.1. Sample collection

We focused sampling on the three major locations of the commercial

fishery for *T. lepturus* in NSW, one of which is also an important recreational fishing location for the species. There were two estuarine sites and one coastal site: (1) the Hawkesbury River estuarine site (33.55° S; 151.33° E); (2) the Hunter River estuarine site (32.93° S, 151.78° E) and; (3) the Hunter River coastal site (32° S – 33° S, 151.80° E – 152.65° E) (Fig. 1).

We sampled 439 *T. lepturus* individuals from the NSW commercial and recreational fisheries during a 16-month period, between September 2015 and December 2016. From the commercial fishery, we aimed to collect a random sample of 10 fish from each of the three sites every two weeks; however, availability varied depending on the operations of the fishery. Sampling was conducted at two seafood cooperatives, which provided access to all *T. lepturus* caught by the commercial fishery at the three study sites. A donation of 46 individuals was also provided by the Commercial Trawl Fishery Observer Program run by NSW Department of Primary Industries (DPI) – Fisheries. These individuals were caught as bycatch in four commercial trawl events occurring in March, May, June and August of 2016.

From the recreational fishery, we obtained 83 samples from an annual recreational fishing competition for *T. lepturus*, held during the 1st – 3<sup>rd</sup> of July 2016 at the Hawkesbury River estuarine site. A second contribution of 32 recreationally-caught samples was provided by the NSW DPI – Fisheries Compliance Unit, following a seizure. All compliance samples were caught between mid-February and mid-April 2016 at the Hunter River estuarine site.

We confirmed all the specimens collected during the present study as *T. lepturus* by examination of their diagnostic characteristics including: grey-coloured dorsal fin (Wang et al., 2017) and morphometrics such as the horizontal distance between the posterior margin of the dermal eye and the first dorsal fin origin at an approximate length of 129% of the eye diameter, and the lack of a dorsal margin of concave head (Chakraborty et al., 2005; Tzeng et al., 2007). We recorded the pre-anal length (PL) of each individual to the nearest cm rounding down, which is the

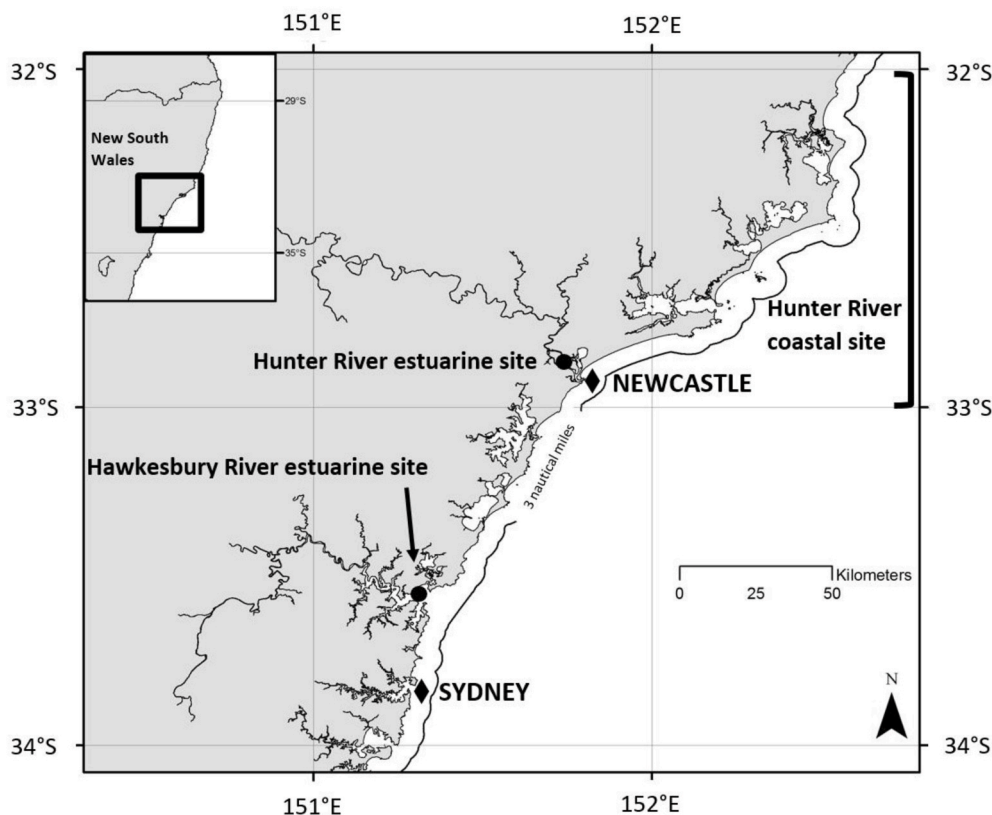


Fig. 1. Map of the south-eastern Australian coast showing the three sites from which *Trichiurus lepturus* were sampled between September 2015 and December 2016.

**Table 1**

Macroscopic and microscopic characteristics of male and female gonads of *Trichiurus lepturus*, following the methods of Abou Shabana (2012), Das Neves et al. (2019), Kwok and Ni (1999), Martins and Haimovici (2000), Johnson et al. (2009, p. 96), Stewart (2011, p. 257), Qamar et al. (2018) and Qamar et al. (2020).

Female		
Stage	Macroscopic characteristics	Microscopic characteristics
1. Juvenile	Gonads are a small thread-like strand. No eggs visible. Difficult to determine sex.	Tissue is made up of primary growth oocytes, chromatin nucleolar and perinucleolar oocytes, the nucleus takes up a large proportion of these small cells. At the later stage of primary growth, nucleoli form at the periphery of the nucleus.
2. Developing/ resting	Ovaries occupy approximately 50–70% of the ventral cavity. Orange in colour and tube-like shape allows an obvious distinction of female ovaries from male testes. Oocytes are not visible through the ovarian wall.	Cortical alveolar oocytes have developed. The first small yolk granules are forming in the cytoplasm. Primary growth oocytes are still present.
3. Mature/ripe	Ovaries usually extend the full length of the ventral cavity. Orange colour and tube-like shape. Oocytes are visible through the ovary wall. Oocytes are opaque.	Vitellogenic oocytes have developed. There are more yolk granules in the cytoplasm and they are increasing in size. In the later stages the yolk begins to fuse together and migrates toward the edge of the cell.
4. Spawning (running ripe)	Ovaries usually extend the full length of the ventral cavity. Hydrated ova can be seen through the ovary wall. Oocytes are large and almost translucent. Oocytes are shed when gentle pressure is applied to abdomen.	Hydrated (spawning/running ripe) oocytes are large and appear uniform due to the cell being filled with the fused, hydrated yolk mass.
5. Spent	Pale violet in colour. Flaccid and bloodshot.	Tissue is predominantly made up of post ovulatory follicles, difficult to distinguish from stage 2.
Male		
Stage	Macroscopic characteristics	Microscopic characteristics
1. Juvenile	Gonads are a small thread-like strand. Difficult to determine sex.	Spermatogonia are predominant in the tissue contained within spermatogenic cysts. There is initial development of spermatocytes and spermatids.
2. Developing	Testes are approximately 50–70% of the ventral cavity. Pale pink colour. Mostly translucent. Obvious distinction of male testes from female ovaries.	Tissue predominantly made up of spermatocytes contained within spermatogenic cysts. Testis may contain spermatogonia, and spermatids. Spermatozoa may have developed.
3. Mature/ripe	Testes usually extend the full length of the ventral cavity. Pale pink or cream colour. Opaque and milky. There is an obvious tapered edge that runs along the length of the testes.	Tissue predominantly made up of spermatids contained within spermatogenic cysts. spermatogonia, spermatocytes may also be present and spermatozoa may have developed.
4. Spawning (running ripe)	Testes usually extend the full length of the ventral cavity. Pale pink or cream colour. Opaque and milky. There is a discernible tapered edge that runs along the length of the testes. Milt is shed through anal vent when gentle pressure is applied to the abdomen.	Larger proportion of tissue has developed into spermatozoa. Spermatids have developed further.
5. Spent	Pale violet in colour. Flaccid and bloodshot.	Reduced volume of residual spermatozoa.

measurement from the anterior extremity of the lower jaw to the anal vent. Pre-anal length is a more reliable length measure than total length (TL) because the thin tail of *T. lepturus* is prone to damage (Al-Nahdi et al., 2009; Khan, 2006). We used the relationship between PL and TL of 362 intact fish to estimate the TL of all individuals ( $TL = 2.254 \times PL + 17.322$ ,  $R^2 = 0.9637$ ), to allow for comparisons with results from other studies that have reported TL. Additionally, we recorded the wet body weight and wet gonad weight of each intact individual and assigned sex for 367 of the individuals based on the presence of identifiable ovaries or testis. We compared the length-frequency distributions of male and female *T. lepturus* using a Kolmogorov-Smirnov test.

## 2.2. Estimating maturity

We used the macroscopic characteristics of gonads to assign a categorical stage between 1 and 5, following the criteria shown in Table 1 (Martins & Haimovici, 2000). We verified maturity stages by identifying the microscopic characteristics of a subset of gonads from each sampling site, each sex, and a range of lengths from each of the maturity stages. Following standard histological techniques (Humason, 1979), the gonad tissue was stored in a fixative solution of 10% formaldehyde then rinsed in water followed by 70%, 90% and absolute ethanol, then clarified with xylene. Tissue was processed in an automatic tissue processor (ASP200S – Vacuum Tissue Processor, Leica, Wetzlar, Germany) and embedded in paraffin wax (EG1150H – Paraffin Embedding Station, Leica and Paraplast Plus, Leica, Wetzlar, Germany) before a 5 µm cross-section was cut through the middle using a microtome (RM2145 Microtome, Leica, Wetzlar, Germany). Histological sections were mounted onto glass microscope slides using adhesive (Ultramount No 9, Forrestdale, Australia) and stained with haematoxylin and eosin. Sections were examined and imaged to 40× magnification using a digital whole slide scanner (Aperio AT2 Scanner, Leica, Wetzlar, Germany) and images of each gonad were

taken using image analysis software (Aperio eSlide Manager, Leica, Wetzlar, Germany).

## 2.3. Length at maturity

We considered macroscopic gonad Stages 1 and 2 as immature and Stage 3 and above as mature, which was consistent with previous studies of *T. lepturus* (Al-Nahdi et al., 2009; Martins & Haimovici, 2000). To estimate the length at which 50% of individuals were mature ( $L_{50}$ ), we calculated the proportion of fish assigned as mature in each 1 cm length-class and fitted a logistic curve to the data using a non-linear least squares procedure in Microsoft Excel (Solver). We estimated  $L_{50}$  for males and females separately and compared the values and logistic curves using the bivariate form of Wald's F-test in "R" (Version 3.4.3) (Kotz et al., 1982) following the methods of Hughes and Stewart (2006).

## 2.4. Spawning period

We estimated the spawning period by investigating the timing of reproductive activity. We examined the gonadosomatic index (GSI) (gonad weight as a percentage of gonad free body weight) across months for all the mature male and female individuals where it was possible to record a gonad weight. Also, we used trends in gonadal stages to support the results from the GSI, by calculating the monthly proportions of individuals at different maturity stages for all individuals for which gonad staging was possible. For both analyses, we used individuals greater than the length at 50% maturity estimated in the current study (40 cm PL or 108 cm TL), to minimise the potential confounding effect of juveniles on temporal patterns.

## 2.5. Sex ratio

We investigated sex ratio of *T. lepturus* by season (spawning and non-spawning) and habitat (estuarine and coastal). The habitat investigation was restricted to samples outside of the spawning period. We used Chi-squared goodness-of-fit tests to investigate whether sex ratio deviated from a ratio of 1:1 during the spawning period and the non-spawning period. The tests were done for both the Hunter River coastal site and the Hunter River estuarine site. Additionally, we investigated sex ratio at the small temporal and spatial scale of individual catch events (defined as a catch made by a commercial fisher on a single day and at a single location) using a Chi-squared test of independence (SPSS v 3.2). This analysis tested whether observed numbers of males and females differed from that expected if there was no pattern across catch events.  $P < 0.05$  was considered significant for all tests.

## 3. Results

### 3.1. Length composition and maximum length

Individuals ranged from 12 to 78 cm PL (44–193 cm TL), with most individuals (87%) between 30 and 60 cm PL. Length-frequency distributions differed between males and females (Fig. 2, Kolmogorov-Smirnov test,  $D = 0.16$ ,  $P = 0.002$ ). Females had a smaller modal body length than males (females: 31–35 cm PL, males: 41–45 cm PL), but a greater length range (females: 12–78 cm PL, males: 30–56 cm PL) and larger maximum length (females: 78 cm PL/193 cm TL, males: 56 cm PL/139 cm TL).

### 3.2. Gonadal maturation

We used histological sections to verify the macroscopic staging for males and females. The macroscopic and microscopic characteristics of male and female gonads, following the methods of (Kwok & Ni, 1999), Martins and Haimovici (2000), Johnson et al. (2009, p. 96), Qamar et al. (2018) and Qamar et al. (2020) are detailed in Table 1. Histological sections of female ovaries, stage 1–4 are displayed in Fig. 3 a – d. Histological sections also revealed multiple oocyte development stages were present in the same ovary, including hydrated (spawning/running ripe) oocytes occurring alongside developing oocytes (Fig. 3d).

Histological sections of male testes, stage 2–3 are displayed in Fig. 4

a – b. Male stage 1, juvenile testes, stage 4, running ripe testes, and Stage 5, spent testes, were absent from the collection.

### 3.3. Length at maturity

The estimated lengths at which 50% of females and males reached sexual maturity ( $L_{50}$ ) were 40.2 and 40.6 cm PL (108 and 109 cm TL), respectively (Fig. 5). The logistic curves describing maturity as a function of length for males and females were significantly different (Fig. 5, Wald's test,  $P < 0.05$ ); however, the  $L_{50}$  values had overlapping standard errors (Female  $40.2 \pm 0.8$  cm; males  $40.6 \pm 2.8$  cm). The selection range, i.e. the PL between 25% and 75% probability of being mature, was  $8.90 \pm 0.1$  cm and  $31.5 \pm 11.4$  cm for females and males, respectively. We fitted a logistic curve to the combined data across both sexes and the estimated  $L_{50}$  was  $40.3 \pm 0.7$  cm PL (108.2 cm TL).

### 3.4. Spawning period

Mean GSI calculated for female *T. lepturus* pooled over the collection locations began to increase in March and remained relatively high between May and September, with the highest value recorded in August at 3.5%. It then declined rapidly up until October. The lowest values were recorded between January and February at 0.2% and 0.3%, respectively. The mean GSIs for males were generally lower than for females. No males were available in August, but during the other months, there was an extended period of slightly elevated values (0.5%–1%), relative to the lower values in January and February at 0.2% and 0.3%, respectively (Fig. 6). Macroscopic maturity staging for male and female gonads indicated a similar pattern of reproductive activity to that of GSI. Stage 4 (running ripe) ovaries were only observed during the suggested spawning period from March to September. In the months outside of the spawning period window, only Stage 2 (developing/resting) and stage 3 gonads (mature/ripe) were observed (Fig. 7).

### 3.5. Sex ratio

Most *T. lepturus* observed from NSW were female, with a F: M sex ratio of 1: 0.4. Based on chi-square test of goodness of fit test we found there were significantly more females than males in both the spawning ( $\chi^2$ :  $df = 1$ ,  $P < 0.001$ ) and non-spawning ( $\chi^2$ :  $df = 1$ ,  $P < 0.001$ ) period and there were significantly more females than males in both estuarine

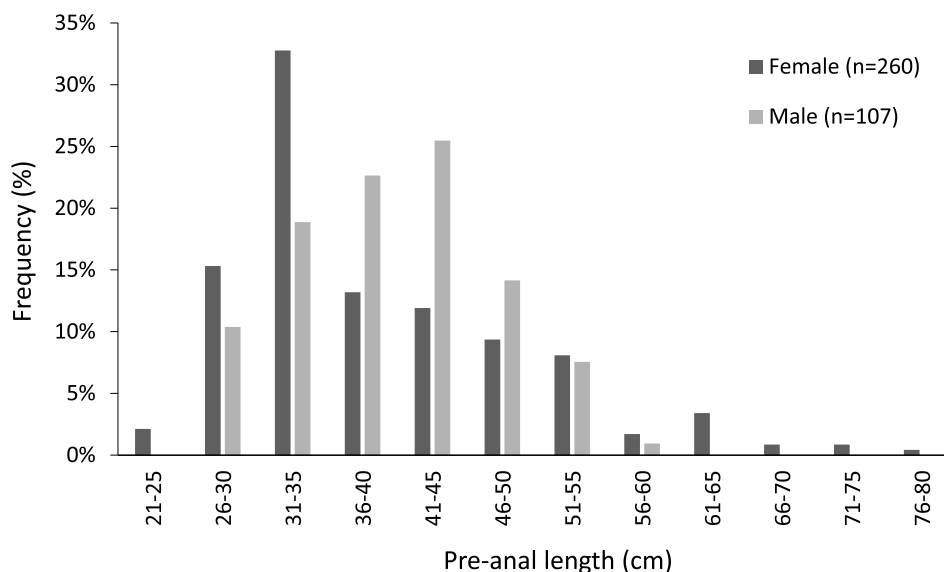
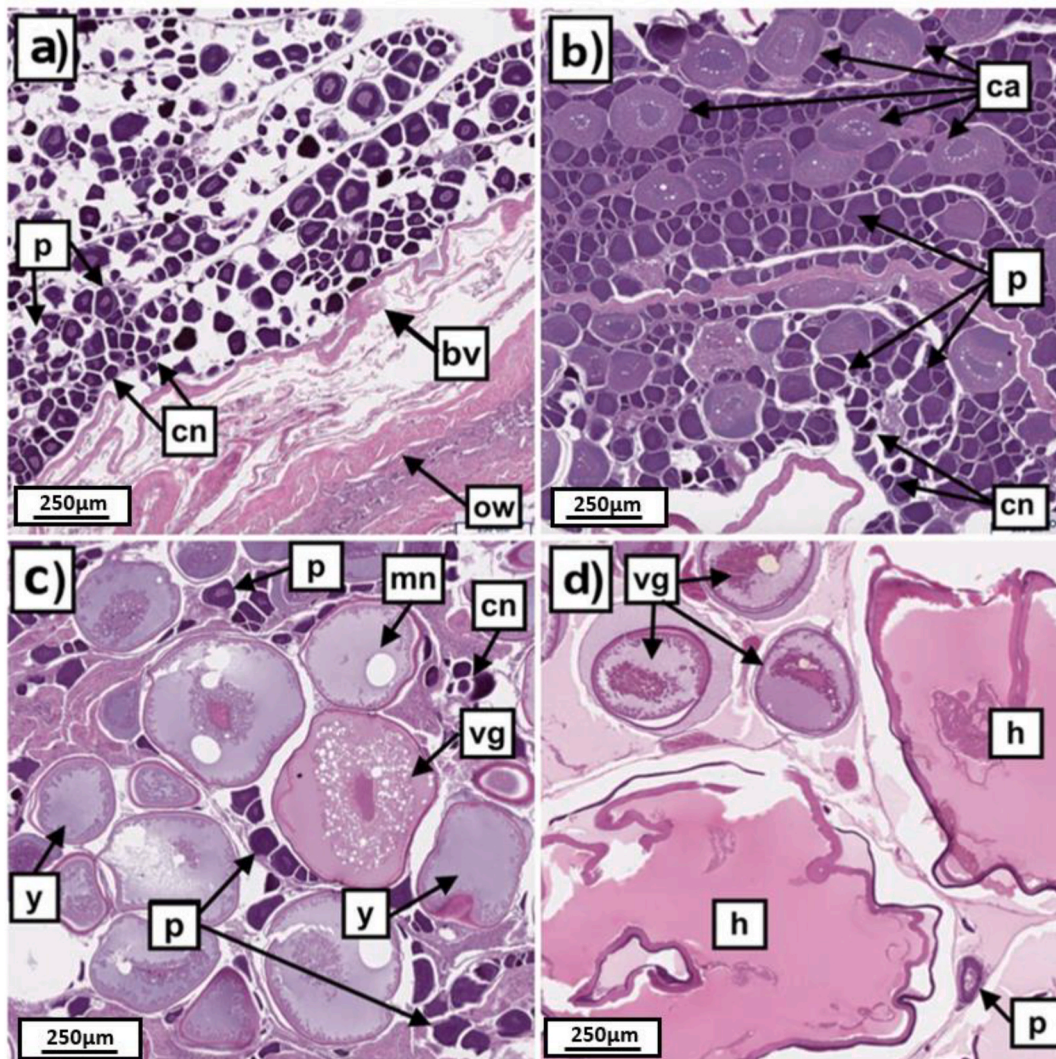


Fig. 2. Length frequency distributions of male and female *Trichiurus lepturus* collected from the commercial fishery in south-eastern Australia between September 2015 and December 2016. Individuals are from all three collection sites and all fishing methods. Only individuals that could be macroscopically assigned to a sex were included.



**Fig. 3.** Histological sections of *Trichiurus lepturus* ovarian tissue according to the criteria detailed in Table 1 a) stage 1 (juvenile), b) stage 2 (developing/resting), c) stage 3 (ripe), and d) stage 4 (running ripe). Abbreviations: **cn**, chromatin nucleolar oocyte; **p**, perinucleolar oocyte; **bv**, blood vessel; **ow**, ovarian wall; **ca**, cortical alveolar oocyte; **vg**, vitellogenic oocyte; **y**, fused yolk; **mn**, migratory nucleus oocyte; **h**, hydrated oocyte.

( $\chi^2$ :  $df = 1$ ,  $P < 0.001$ ) and coastal habitats ( $\chi^2$ :  $df = 1$ ,  $P < 0.001$ ). A chi-square test of independence revealed there was significant variation in the sex ratio among catch events ( $\chi^2$ :  $df = 4$ ,  $P < 0.001$ ). Some of the catch events were entirely female and this was observed in catches during both the spawning period and outside the period. Twelve out of 17 catch events were mostly females, and five catch events were mostly male, three of which were taken outside the spawning period (Table 2).

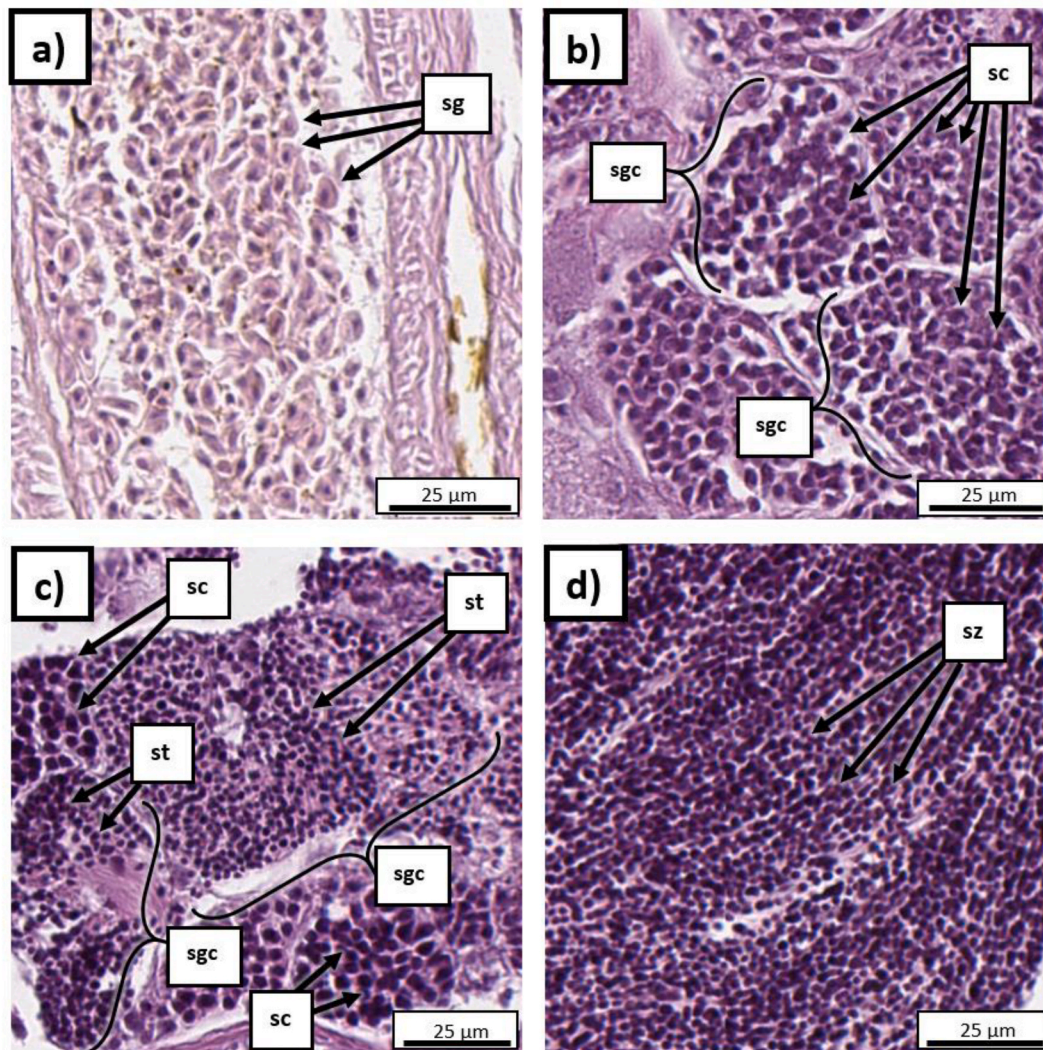
## 4. Discussion

### 4.1. Maximum lengths

The maximum length (78 cm PL/193 cm TL) for *T. lepturus* from south-eastern Australia was substantially larger than that reported from other global regions, except the maximum length reported by Shih et al. (2011) from Taiwan, which was similar to the current study (79 cm PL). Other regions reported smaller maximum lengths including 126 (Ghosh et al., 2009), 124 (Khan, 2006), 114 (Abdussamad et al., 2006) and 101 cm TL from India (Reuben et al., 1997), 126 cm TL from Oman (Al-Nahdi et al., 2009), 160 cm TL from southern Brazil and 30 cm PL from Puerto Rico (Del Toro, 2001). The larger maximum length recorded in the current study may be the result of intrinsic differences in growth

between sub-populations of the *T. lepturus* complex (Shih et al., 2011). Alternatively, the larger maximum length may be related to differences in fishing pressure among regions. Lower fishing pressure in south-eastern Australia may have resulted in retention of larger length classes relative to regions of higher fishing pressure, where length structures may already be truncated (Carter et al., 2015; Law, 2000; Tu et al., 2018). The larger females observed in south-eastern Australia may yield greater reproductive output than females in other regions, given the positive relationship between body length and fecundity observed for *T. lepturus* in the Bay of Bengal and the northern Arabian Sea, off India (Ghosh et al., 2014). Further investigation into the growth rates and fecundity of stocks is necessary to investigate whether the larger maximum length was an indication of productivity in the population.

Length distributions of *T. lepturus* in south-eastern Australia differed between males and females, and all individuals larger than 56 cm PL were female, suggesting that females in the south-eastern Australian population may grow larger than males. This result is consistent with reports of females reaching larger lengths in India (Reuben et al., 1997) and Puerto Rico (Del Toro, 2001), which are the only other studies to report maximum length by sex. Alternatively, large males may have been missed in our sampling due to spatial segregation and the limited spatial extent of fishing in the current study, which was primarily



**Fig. 4.** Histological sections of *Trichiurus lepturus* testicular tissue according to the criteria detailed in Table 1 a) stage 1 (juvenile), b) stage 2 (developing), c) stage 3 (mature/ripe) and d) stage 4 (running ripe). Abbreviations: sgc, spermatogenic cyst; sg, spermatogonia; sc, spermatocytes; st, spermatids; sz, spermatozoa.

conducted in estuaries and nearshore coastal habitats (Hilborn & Walters, 1992; Stewart et al., 2015). Spatio-temporal segregation of sexes has previously been suggested for *T. lepturus* by Martins and Haimovici (2000) and is discussed for the NSW population in section 4.4.

Small individuals were under-represented in our sampling, potentially because the gear used by recreational anglers and commercial handline fishers is selective of larger length classes (Boukal et al., 2008; De la Cruz-Torres et al., 2014). In addition, small individuals landed by commercial trawl vessels are often not retained for market, due to their fragility and the damage sustained during capture, according to reports from trained observers onboard coastal trawl vessels in NSW (C. Clain, pers. comm.). Alternatively, small individuals may be spatially segregated from larger individuals, potentially due to different habitat requirements (Sather et al., 2016). Fishery-independent sampling using alternative gear types, or collections from the discards of commercial gear such as prawn trawls, which have relatively fine mesh compared to fish trawls, may increase the proportion of smaller individuals in future sampling.

#### 4.2. Length at maturity

The difference in the length-at-maturity ogives observed between males and females in south-eastern Australia was likely driven by the considerable difference in the steepness of the logistic curves, defined by

the selection range (PL between the 25% and 75% probability of being mature on the fitted logistic curve), because there was little difference in the  $L_{50}$  estimate between sexes. The difference in steepness may have been driven by the under-representation of large males, causing the logistic curve fitted to male data to be less steep than the curve fitted to female data, rather than a biological difference in the length range of maturation between sexes. The absence of males larger than 55 cm PL may be an inherent feature of the south-eastern Australian population, as discussed in section 4.1. However, the lack of a length class at which 100% of males were mature suggests under-sampling of larger males is more likely. Future sampling should increase effort to ensure collection of large males, if they are present in the population, although a sex ratio skewed toward females may render this challenging (see section 4.4).

The length at which 50% of *T. lepturus* individuals from south-eastern Australia reached sexual maturity ( $L_{50}$ ) was substantially larger than the stocks of *T. lepturus* from all other regions including 35 cm TL for females from Mexico (Sheridan et al., 1984), 59 cm TL for females from Japan (Munekiyō & Kuwahara, 1984), 69 cm TL for females from southern Brazil (Martins & Haimovici, 2000), 26 cm PL for females from China (Kwok & Ni, 1999) and 61 cm TL for combined sexes from India (Ghosh et al., 2014). Although length at maturity varies among regions, the value from the current study is 28% larger than the next largest value reported from the Arabian Sea off Oman at 79 cm PL (Al-Nahdi et al., 2009). The large length at maturity is consistent with the assertion of

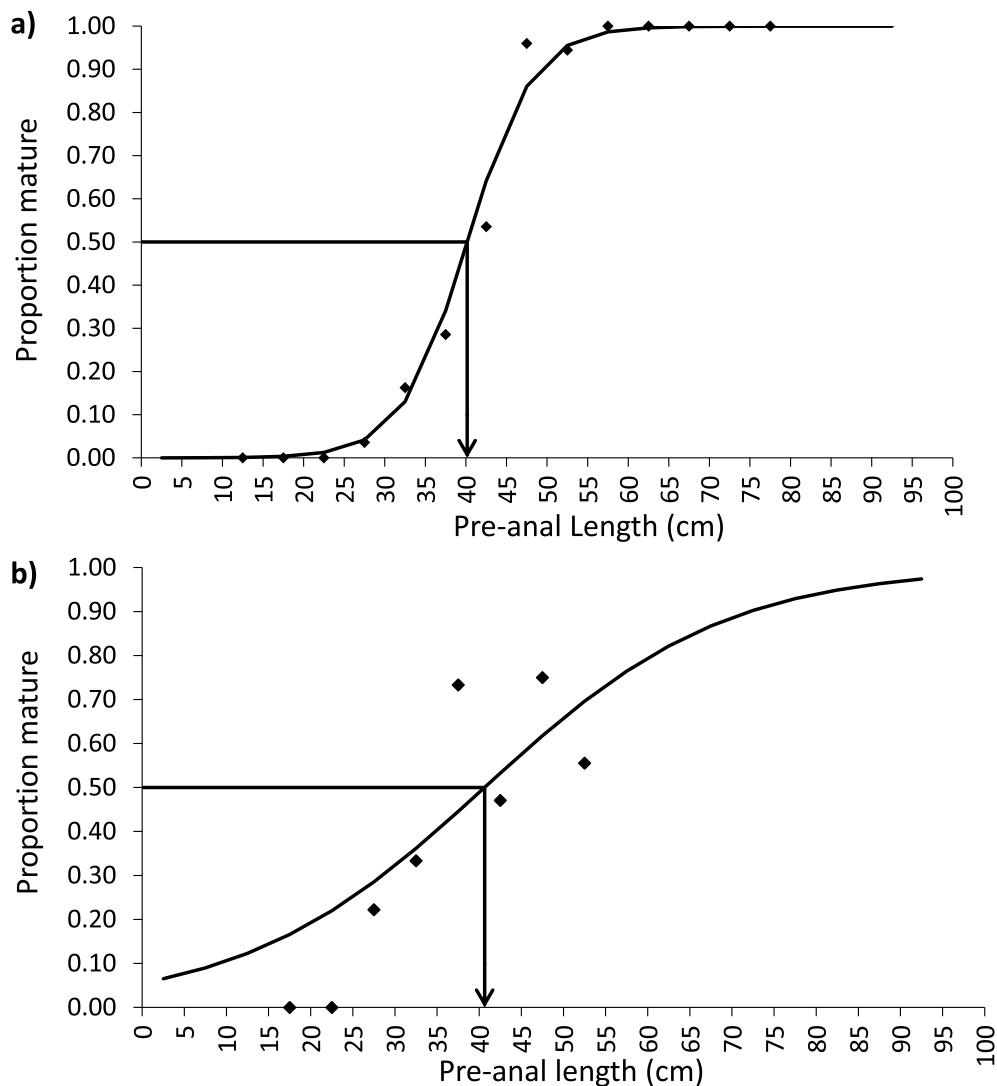


Fig. 5. Length at maturity data with fitted logistic curves for *Trichiurus lepturus* collected from NSW between September 2015 and December 2016 for a) females,  $R^2$  value = 0.97 and b) males,  $R^2$  value = 0.75. The solid arrows indicate the length at 50% maturity.

Martins and Haimovici (2000) that the life history strategy of *T. lepturus* varies greatly with geographic location and the assertion of Al-Nahdi et al. (2009) that *T. lepturus* from environments with marked temperature cycles or lighter fishing pressure are more likely to reach maturity at larger lengths. Al-Nahdi et al. (2009) observed that marked temperature cycles and lighter fishing pressure have been reported from the regions of Japan, the South China Sea, southern Brazil and the Arabian Sea off Oman, but not from the Gulf of Mexico or India; the reported lengths at maturity for *T. lepturus* are larger from the former group of regions relative to the latter. Length at maturity in the current study is consistent with this pattern, with the study region in south-eastern Australia having minimal fishing pressure relative to other regions and relatively large seasonal temperature fluctuations given the temperate latitude (Stewart et al., 2015; Suthers et al., 2011). At present, the relatively low fishing yield for *T. lepturus* in NSW implies that fishing pressure may have had less of an impact on the length-at-maturity of the stock compared to the heavily fished regions in the north-west Pacific. However, with increasing demand for seafood (FAO, 2018), the fishing pressure for *T. lepturus* in Australia may increase in the future (Coulson et al., 2012). Results from the current study may provide a useful baseline for the length at maturity of a stock prior to substantial exploitation. Another possible explanation for the global variation in length at maturity could be restricted connectivity resulting in varied

genetic or demographic population structure (Shih et al., 2011).

#### 4.3. Spawning period

The estimated spawning period for *T. lepturus* in south-eastern Australia is similar in duration to some reported from other regions (Table 3). In addition to the peak spawning period which occurred during the Austral winter, between May to September, *T. lepturus* demonstrated seven months of gonadal activity between March and September. Our findings do not support the model previously suggested by Al-Nahdi et al. (2009) of global variation driven by latitude and water temperature. Al-Nahdi et al. (2009) suggested the spawning period of *T. lepturus* is flexible in populations at low latitudes and warm regions like the Arabian Sea and the Bay of Bengal off the south coast of India and the Gulf of Mexico, whereas at higher latitudes (30°–35° N), spawning periods are more defined and take place from spring to summer. Martins and Haimovici (2000) reported the spawning period of *T. lepturus* in southern Brazil (30°–35°S) takes place from spring to summer. While south-eastern Australia (32°–34°S) is similar in latitude and environmental characteristics to southern Brazil, we estimated the spawning period occurred during the opposite time of year. Again, an alternative explanation for the global variation in spawning periods is potentially stock structure, within which spawning periods diverged. An

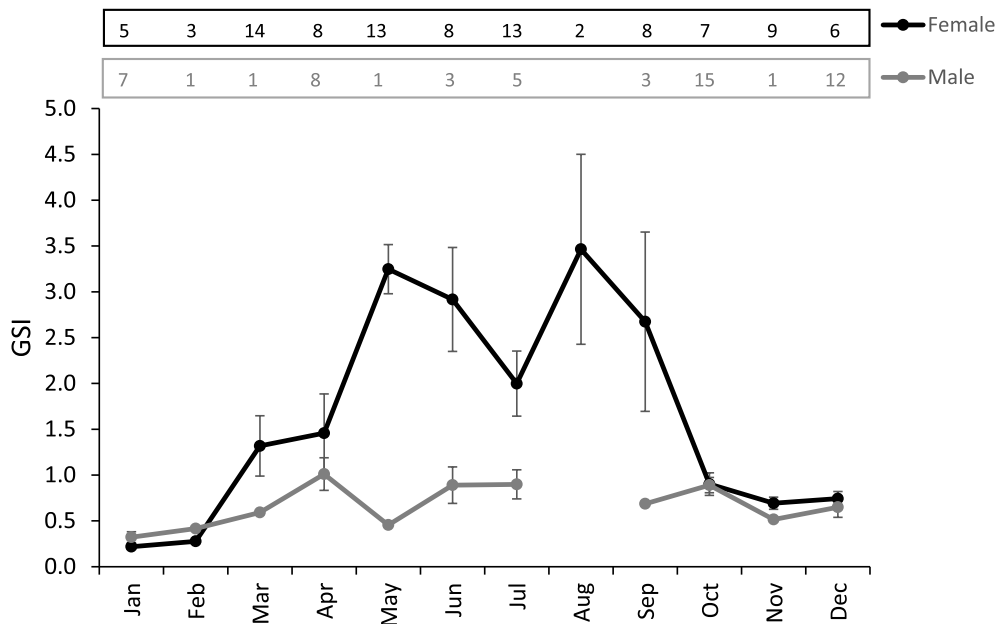


Fig. 6. Monthly variation in gonadosomatic index (mean ± SD) of mature sized *Trichiurus lepturus* collected from NSW between September 2015 and December 2016. Numbers in black above graph indicate female sample sizes and numbers in grey indicate male sample sizes.

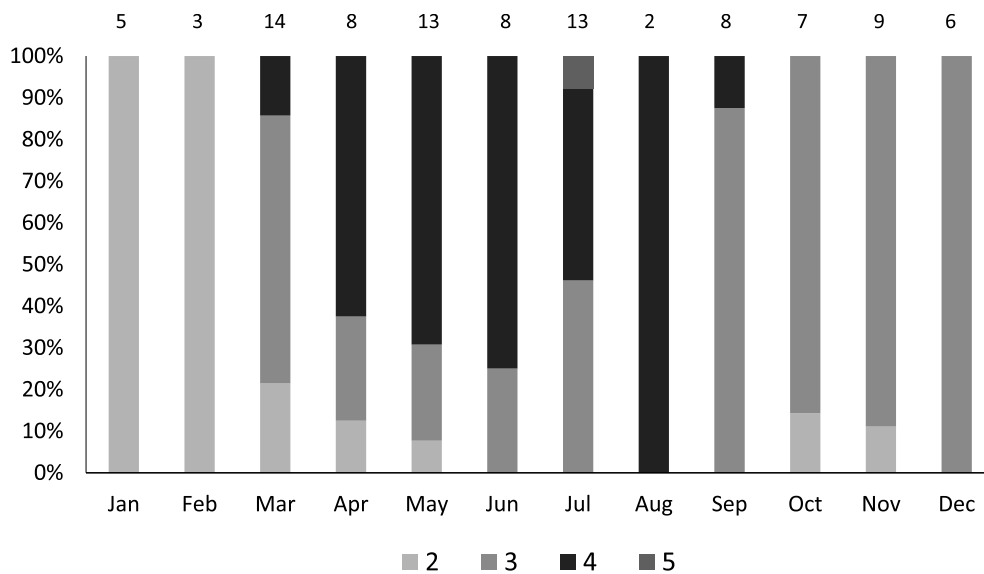


Fig. 7. Monthly variation in female ovary macroscopic maturity stages for mature sized *Trichiurus lepturus* collected from the NSW commercial fishery between September 2015 and December 2016. Numbers above columns represent sample sizes.

investigation of potential population structure among regions using multiple population markers would be useful for testing this model (Izzo et al., 2017), and may provide insight into a range of divergent reproductive traits reported across regions.

We observed oocytes at various stages of development within individual ovaries, indicating that *T. lepturus* in south-eastern Australia are likely asynchronous batch spawners (Del Toro, 2001). Our finding is similar to those for most regions, with batch spawning for the species reported from the Caribbean Sea off south-west Puerto Rico (Del Toro, 2001), the Arabian Sea off central western India (Khan, 2006), the Arabian Sea off north western India and the Bay of Bengal off north-eastern India (Ghosh et al., 2014), both the East and South China Sea off China (Kwok & Ni, 1999), and the Atlantic Ocean off south eastern Brazil (Martins & Haimovici, 2000).

#### 4.4. Sex ratio

Sex ratio for *T. lepturus* in south-eastern Australia were skewed towards females, similar to stocks in other regions. Such female domination in *T. lepturus* stocks has been reported from the Caribbean Sea off south-west Puerto Rico (Del Toro, 2001), the Arabian sea off Oman (Al-Nahdi et al., 2009), The Gulf of Mexico off Boca del Rio in Mexico (De la Cruz-Torres et al., 2014), the northern Arabian Sea and northern Bay of Bengal off India (Ghosh et al., 2014) and the Atlantic Ocean off southern Brazil (Martins & Haimovici, 2000). In the current study, we observed significantly more females than males in both the spawning and non-spawning period and there were significantly more females than males in both estuarine and coastal habitats. These observations are inconsistent with those from southern Brazil, where sex ratio varied between time periods and habitats (Martins & Haimovici, 2000). In



**Table 2**

Sex ratio by catch event for *Trichiurus lepturus* collected from the commercial trawl and handline fishery in south-eastern Australia between September 2015 and December 2016. The shaded rows indicate the catch events that occurred during the spawning period. All the catch events with >6 individuals from the Hunter River estuarine site and Hunter River coastal site were included. F = female. M = male.

Catch number	Month	Site	Method	F:M	n
1	1	Hunter River Estuarine	Handline	1: 0.5	9
2		Hunter River coastal	Handline	1: 0.4	13
3	2	Hunter River coastal	Handline	1: 0.1	10
4	3	Hunter River Estuarine	Handline	1: 0	19
5	4	Hawkesbury River Estuarine	Prawn trawl	0.6: 1	13
6		Hunter River Estuarine	Handline	1: 0.1	13
7	5	Hawkesbury River Estuarine	Prawn trawl	1: 0.3	19
8		Hunter River Estuarine	Handline	1: 0.6	31
9		Hunter River coastal	Ocean Trawl	1: 0.1	21
10	6	Hunter River coastal	Handline	1: 0.2	7
11	8	Hunter River coastal	Fish trawl	1: 0	10
12	9	Hunter River coastal	Fish trawl	1: 0.4	10
13	10	Hunter River Estuarine	Handline	0: 1	10
14		Hunter River Estuarine	Handline	0.8: 1	11
15		Hunter River coastal	Fish trawl	0.8: 1	7
16		Hunter River coastal	Handline	1: 0	11
17	12	Hunter River coastal	Handline	0.5: 1	19

**Table 3**

Spawning period (shaded months) of *Trichiurus lepturus* across regions. Spawning period was identified using various methods including: GSI<sup>1, 3, 5, 7, 11, 12</sup>; gonad macroscopic maturity staging<sup>6, 8, 9</sup>; recruitment pattern<sup>4, 8</sup>; CPUE<sup>10</sup>. Table values indicate the average temperature of the region in Degrees Celsius (Cheng et al., 2001).

Citation	Country	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<sup>1</sup> Bryan 2007	US (26°N)	24°	25°	26°	28°	30°	31°	32°	32°	32°	30°	27°	25°
<sup>2</sup> Ye and Rosenberg, 1991	China (26°N)	25°	28°	28°	28°	28°	25°	21°	17°	16°	15°	18°	22°
<sup>3</sup> Kwok and Ni 1999	China (26°N)	25°	28°	28°	28°	28°	25°	21°	17°	16°	15°	18°	22°
<sup>3</sup> Kwok and Ni 1999	China (22°N)	25°	28°	28°	28°	28°	25°	21°	17°	16°	15°	18°	22°
<sup>4</sup> Ghosh 2009	India (20°N)	28°	28°	30°	32°	30°	31°	29°	28°	29°	32°	32°	29°
<sup>5</sup> De la Cruz-Torres et al., 2014	Mexico (19°N)	22°	22°	24°	26°	28°	28°	27°	28°	27°	26°	24°	22°
<sup>6</sup> Khan 2006	India (18°N)	28°	28°	28°	29°	30°	32°	29°	29°	30°	32°	32°	30°
<sup>7</sup> Al-Nahdi 2009	Oman (17°N)	22°	23°	26°	29°	31°	31°	29°	28°	28°	28°	26°	23°
<sup>8</sup> Abdussamad 2006	India (16°N)	23°	26°	28°	31°	32°	32°	29°	29°	29°	28°	25°	23°
<sup>9</sup> Tampi 1968	India (13°N)	33°	32°	31°	30°	30°	28°	26°	25°	24°	26°	27°	30°
<sup>10</sup> Cheng 2001	Indonesia (7°S)	27°	26°	25°	26°	26°	27°	28°	28°	28°	28°	28°	27°
<sup>11</sup> Martins 2000	Brazil (33°S)	25°	24°	22°	19°	16°	15°	15°	17°	18°	20°	23°	22°
<sup>12</sup> Current study	Australia (33°S)	22°	22°	21°	18°	14°	12°	11°	12°	15°	18°	19°	21°

Brazil, Martins and Haimovici (2000) observed female domination in stocks of *T. lepturus* in autumn and winter (outside the spawning period), but an even sex ratio during spring and summer (during the estimated spawning period). Martins and Haimovici (2000) suggested males had moved offshore or northward to participate in prolonged spawning periods in other regions. They suggested the population was dividing and implementing two different reproductive strategies, which could mediate potential risks posed by environmental perturbation. In the current study however, females dominated the sex ratio across habitats

and between the spawning and non-spawning periods. Also, in the current study, the sex ratio across most of the sampled catch events were dominated by females. It is possible that males were located primarily outside of the current sampling areas and sex segregation between habitats or locations may have become apparent with broader sampling effort.

We found significant variation in the sex ratio among catch events from the commercial fishery, suggesting that sexual segregation may occur at a small spatial or temporal scale. Four out of five catch events

that were predominantly male occurred within the last three months of the year (October to December), i.e. outside of the spawning period. This suggests sex segregation may be unrelated to immediate reproduction. The potential under-sampling of large males in the current study (see section 4.1) may also have been driven by sex segregation, with large segregated males not being intercepted by fishing effort. De la Cruz-Torres et al. (2014) suggested that the uneven sex ratio between catch events observed in their study might relate to fishing gear, where catches made by the trawl fishery are smaller in length and majority male whereas catches by the line fishery are larger in length and majority female. However, gear selectivity is unlikely to explain the lack of large males in our study because, of the five catch events in our study that were predominantly male, three were from the handline fishery and two were from the trawl fishery. This suggests that males are at least caught by both primary commercial fishing methods in the region. A longer sampling period including more catch events, and more individuals in each catch event, would be required to make a more comprehensive assessment of small-scale sex segregation.

## 5. Conclusions

Our study provides the first information on the life-history traits of *T. lepturus* in south-eastern Australia, which is important for ensuring sustainable management of the stock in the region. We also identified considerable differences in the life-history traits between south-eastern Australia and other regions. While the exact cause(s) of these differences could not be elucidated here, some potential explanations include: 1) lower fishing pressure; 2) demographic or genetic structure arising from geographic isolation; 3) different natural and anthropogenic influences on reproductive traits; 4) past investigations comprising multiple *Trichiurus* spp., or; 5) possible under-representation of smaller length-classes or males in our study. Future research should commence with an investigation of potential population structure among regions, to test a model of restricted connectivity and resulting demographic structure. Subsequent investigations can then explore potential effects of fishing and environmental pressures on reproductive traits.

## CRedit authorship contribution statement

**Chantelle Clain:** Data curation, Project administration, Conceptualization, Methodology, Formal analysis, Investigation, Funding acquisition, Writing – original draft, The material preparation, data curation, project administration and the original draft preparation. All authors contributed to the study conceptualization, design, methodology, the formal analysis, investigation and funding acquisition. All authors read and approved the final manuscript. **John Stewart:** Data curation, Project administration, Conceptualization, Methodology, Formal analysis, Investigation, Funding acquisition, Writing – review & editing, All authors contributed to the study conceptualization, design, methodology, the formal analysis, investigation and funding acquisition. All authors read and approved the final manuscript. **Ashley Fowler:** Data curation, Project administration, Conceptualization, Methodology, Formal analysis, Investigation, Funding acquisition, Writing – review & editing, All authors contributed to the study conceptualization, design, methodology, the formal analysis, investigation and funding acquisition. All authors read and approved the final manuscript.

## Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Research technicians at NSW Fisheries collected length frequency data and biological samples from fish Cooperatives.

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