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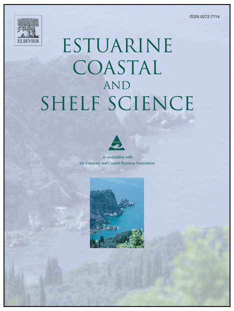

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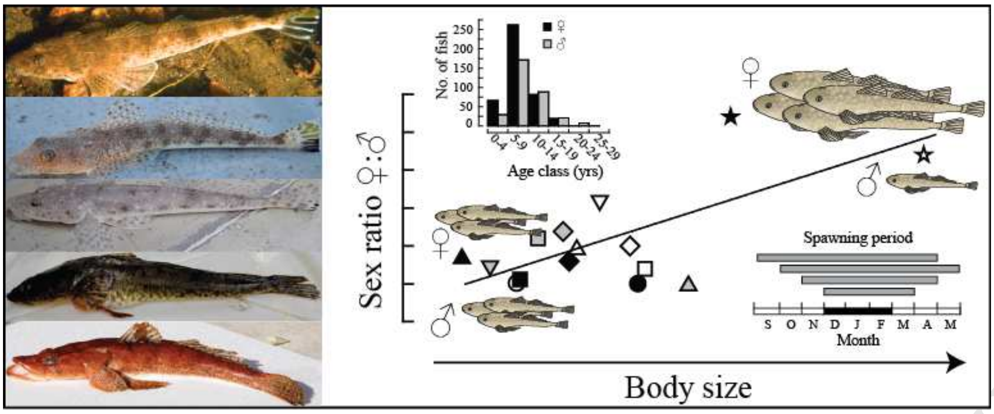
No. of fish
250
200
150
100
50
0
♀
♂
0-4
5-9
10-14
15-19
20-24
25-29
Age class (yrs)
Sex ratio ♀:♂
♀
♂
♀
♂
Spawning period
S O N D J F M A M
Month
Body size

Variations in biological characteristics of temperate gonochoristic species of Platycephalidae and their implications: a review.

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ABSTRACT This review provides a composite account of the biological characteristics of the temperate gonochoristic species of the Platycephalidae. Initially, data were obtained for the five abundant platycephalid species in south-western Australia, which each came from either over bare substrata or seagrass and from either estuaries, marine coastal waters or marine embayments. The von Bertalanffy growth curves for females and males of each species differed significantly, with females having a greater TL_∞ and lower growth coefficient k. From tests using their upper deciles, the total length (TL) attained by the largest females of each species was significantly greater than that of their males, whereas such a trend did not occur with age. The ratio of females to males in each abundant age class, and overall, exceeded parity for four of the five species (typically $P < 0.001$) and increased with increasing TL. Mortality estimates, which were similar for each sex of each species, suggest that *Platycephalus speculator* has been substantially exploited in a seasonally-closed estuary in which it completes its whole life cycle. The above and other biological data for the five species were collated with those published previously for two of those species and five other platycephalid species in south-eastern Australia and one in Japan and another in the Suez Canal, yielding the following conclusions for gonochoristic species of the Platycephalidae. Females attain a larger size than males, the extent varying markedly among species, whereas the longevities of the two sexes of each platycephalid species are similar. The maximum TLs and ages of the various species range widely, with values for females, for example, extending from 221 mm for *Ambiserrula jugosa* to 985 mm for *Platycephalus fuscus* and from four years for *A. jugosa* to 26 years for *Platycephalus conatus*. The overall ratio of females to males is positively related to the extent to which both the maximum TLs and TL_∞s of the females exceed those of males. The above trends imply that growth, rather than differences in longevity and/or mortality, is the main factor contributing to the marked differences in sex ratios, which ranged widely from parity to 3.2:1. As the length at maturity, but not typically age at maturity, was greater for females than males, maturity is also related mainly to growth. The spawning periods of the various species overlapped, commencing as early as late winter/early spring, as temperatures started rising with four species and later in late spring/early summer with the three species found in estuaries, which would be advantageous as spawning in estuaries would occur when environmental conditions are most favourable for spawning success and larval retention.

*Keywords***:** size and age compositions, sex ratio, sexually dimorphic growth, longevity, reproduction, mortality

1. Introduction

The Platycephalidae is found almost exclusively in the Indo-West Pacific (Nelson, 2016), where many of its species are fished commercially and/or recreationally (Masuada, 1991; Gray et al., 2002; Henry and Lyle, 2003; Sabrah et al., 2015; Patterson et al., 2016). This family comprises 18 genera and ~ 80 species, among which 15 genera and ~ 45 species have been recorded in Australian waters and within which 16 belong to the genus *Platycephalus*, which typically have a temperate distribution (Gomon et al., 2008; Imamura, 2015; Nelson, 2016). Although platycephalids are typically gonochoristic, at least two of their species in Japanese waters are protandrous hermaphrodites (Fujii, 1970, 1971; Shinomiya et al., 2003). Comparisons of published data (e.g. Jordan, 2001; Barnes et al., 2011; Gray and Barnes, 2015) suggest that, among platycephalid species in south-eastern Australia, the females tend to grow to a larger size, but not necessarily live longer, than their males. Although the sex ratio typically favours females, the extent of that difference varies among species.

As Wenner (1972) showed, in his seminal review of sex ratios in marine crustaceans, it is important, when discussing sex ratios, to have established whether the ratio of females to males of a species remains similar among length classes or changes in a consistent manner with increasing body size. Wenner (1972) concluded that the specific relationship of the numbers of females to males reflects the ultimate physical sizes that result from factors such as differential growth, longevity and mortality of the two sexes. There has been no attempt, however, to explore statistically whether a tendency for the females of platycephalids to be more numerous than their males is related to their growth to a larger size, lesser mortality and/or greater longevity.

The several platycephalid species studied thus far in the mid-southern and south-eastern Australian coasts are gonochoristic and well represented either over bare substrata or in seagrass located in either coastal marine or estuarine waters (Klumpp and Nichols, 1983; Jordan, 2001; Gray and Barnes, 2015). The studies on *Platycephalus speculator* in south-western Australia (Hyndes et al., 1992a, b), and preliminary unpublished results by the senior author for the other four abundant species in this microtidal region demonstrate that all five of these species are gonochorists. *Platycephalus speculator* completes its life cycle in marine embayments and coastal waters, and in seasonally-closed estuaries, such as Wilson Inlet, in which it is frequently associated with seagrass (Lenanton and Potter, 1987; Hyndes et al., 1992a, b; Potter and Hyndes, 1994, 1999; Gomon et al., 2008). Among the other four abundant species, whose biology has not been studied in detail in south-western Australia, *Platycephalus westraliae*, previously recorded as *Platycephalus endrachtensis* (Imamura, 2008), is numerous over sandy substrata and largely confined to the permanently-open Swan River Estuary (Potter et al., 1990; Potter and Hyndes, 1999). As estuaries are the most productive of marine environments (Schelske and Odum, 1961; Contanza et al., 2007), they facilitate rapid growth of the juveniles of marine species, and thus presumably also of those of estuarine residents, thereby likewise reducing the susceptibility of these young fish to predation (Blaber and Blaber, 1980; Kennish, 1990; Able and Fahay, 2010; Veale et al., 2016). *Platycephalus grandispinis*, previously recorded as *Platycephalus longispinis* (Imamura, 2013), is abundant over bare substrata in protected coastal marine waters on the lower west, south and south-eastern coasts of Australia (Valesini et al., 1997; Platell and Potter, 1998; Barnes et al., 2011), which, on the basis of the densities of its nematode and macroinvertebrate faunas (Wildsmith et al., 2005, 2011; Hourston et al., 2011), are far less productive than the Swan River Estuary. The remaining two abundant species, *P. laevigatus* and *L. inops* are found in large embayments on the south coast of Western Australia, and particularly in association with seagrass (Coulson et al., 2014, 2015), with the former also found in seagrass in south-eastern Australia (Klumpp and Nichols, 1983).

Platycephalus westraliae and *P. speculator*, which attain total lengths (TL) of ~ 1 m (Hutchins and Swainston, 1986), are fished recreationally and commercially (Smith, 2006; Ryan et al., 2015), as are certain other *Platycephalus* species in estuaries and coastal marine waters elsewhere in Australia and in Japan (Gray et al., 2002; Stokie and Talman, 2003; Koopman et al., 2004; Lyle et al., 2007; Barnes et al., 2011). In the context of estuaries, the Estuary Cobbler *Cnidoglanis macrocephalus* in the seasonally-closed Wilson Inlet, which contains one of the largest commercial estuarine fisheries in Western Australia, has been subjected to appreciable exploitation (Chuwen et al., 2011). Although *P. grandispinis* is common in the bycatch of prawn and scallop trawlers in south-western Australia (P. Coulson pers. observ.), it is only occasionally retained because its minimum legal length (MLL) for retention of 300 mm is only slightly less than the maximum TL of 340 mm (Hutchins and Swainston, 1986), a value similar to that for this species in eastern Australia (Barnes et al., 2011). *Platycephalus laevigatus* and *L. inops*, which can attain TLs of ~ 800 and 600 mm, respectively (Hutchins and Swainston, 1986), are caught commercially in large embayments on the south coast of Western Australia (Coulson et al., 2014), with the first also caught commercially in marine embayments on the south coast of eastern Australia (Koopman et al., 2004). Despite the importance of several platycephalid species to certain fisheries, there has been no attempt to use contemporary methods to estimate total and natural mortality of a population of a platycephalid species in south-western Australia or elsewhere.

This review develops a broad and integrated perspective of the key biological characteristics of the temperate, gonochoristic species of the Platycephalidae, which collectively occupy different habitats and environments. Particular emphasis has been placed on elucidating factor(s) that influence those characteristics. Initially, the age and length compositions, growth, sex ratio and reproductive biology of populations of *P. westraliae*, *P. grandispinis*, *P. laevigatus* and *L. inops* in south-western Australia were determined and combined with those collected previously for *P. speculator* in that region (Hyndes et al., 1992a,b). These data, which had all been produced using the same protocols, were employed to confirm that the females in these five populations do not attain a significantly greater age than males, but grow to a larger size. They were also used to explore 1) the hypothesis that early growth in the populations of the two species living in estuaries is greater than in those of the three species occupying coastal marine waters and 2) the possibility that the two estuarine populations have been subjected to detectable exploitation. The biological data for the five species in south-western Australia were then collated with those recorded for several species in this family, in central southern and eastern Australia (Stokie and Talman, 2003; Koopman et al., 2004; Barnes et al., 2011; Gray and Barnes, 2015), Japan (Masuda, 2000) and the Suez Canal (Sabrah et al., 2015). Finally, the data were used to test the hypothesis that the overall sex ratio is positively related to the magnitude of the differences between both the TL_∞ and maximum TLs attained by the females and males.

2. Materials and methods

2.1. Sampling locations and methods and water temperatures

The microtidal estuaries on the lower west coast of Western Australia, such as the Swan River Estuary in which *P. westraliae* was sampled, are almost invariably open to the sea, whereas many of those along its south coast, such as Wilson Inlet from which *P. speculator* was obtained, are either seasonally or normally closed (Hodgkin and Hesp, 1998; Potter and Hyndes, 1999; Chuwen et al., 2009). The permanently-open Swan River Estuary at ~ 32°S (Fig. 1) is the second largest estuary on the lower west coast, occupying ~ 55 km^2, while the seasonally-open Wilson Inlet at ~ 35°S is the largest estuary on the south coast, covering ~ 48 km^2 and containing extensive growths of *Ruppia megacarpa* (Humphries et al., 1992; Brearley, 2005). The latter estuary is typically opened artificially during late winter or spring, when water in the basin rises and threatens to flood low-lying areas along the shoreline (Brearley, 2005).

Platycephalus westraliae was sampled in the Swan River Estuary monthly between August 2004 and December 2006 using 21.5 and 40.5 m seine nets, with 3 and 9 mm mesh in their bunts, respectively, and by rod and line angling. Additional whole and filleted *P. westraliae* were obtained monthly from commercial fishers in the Swan River Estuary in 2005 and further whole fish were purchased from a local wholesale fish market during winter and spring in 2005 and 2006. *Platycephalus speculator* was collected monthly from the basin of Wilson Inlet between September 1987 and April 1989 by using, during the day, a 21.5 m seine with the same dimensions as above, and by employing, at night, a composite sunken gillnet comprising six 21 m long panels, each with a different stretched-mesh ranging from 38 to 102 mm, and an otter trawl with a mesh size of 25 mm in the pocket (see Hyndes et al. (1992a, b) for further details).

Platycephalus grandispinis was obtained from the catches of commercial scallop/prawn trawlers and a fisheries training vessel operating along the lower west coast at ~ 32°S, with smaller fish caught in Comet Bay (10-15 m deep) and larger fish in open waters off Rottnest Island (30-40 m deep) (Fig. 1). The Comet Bay samples were obtained between November 2009 and March 2010 and those from Rottnest Island in April and in August to October of 2008 and in February to May 2009. As the commercial scallop/prawn fishery in the waters off Rottnest Island is closed from November to February, *P. grandispinis* could not be collected during this period from those waters, in which the largest fish were caught. The net used for trawling had a stretched mesh size of 50 mm in the wings and 45 mm in the cod-end (Jones et al., 2008).

The two well enclosed embayments of King George Sound and Princess Royal Harbour, in which *P. laevigatus* and *L. inops* were mainly caught, are on the south coast of Western Australia and just to the east of Wilson Inlet at ~ 35°S (Fig. 1). These embayments contain large and dense beds of the seagrass *Posidonia sinuosa* (Bastyan, 1996; Kirkman, 1987; Kirkman and Kuo, 1990). *Platycephalus laevigatus* and *Leviprora inops*, which had been caught by commercial fishers using gillnets, were collected from fish processors as filleted frames, with their viscera intact, or purchased fully intact from a wholesale market. Both species were obtained at frequent intervals between July 2006 and June 2009, with each calendar month of the year represented by at least one sample. Juveniles of each species were collected from those waters opportunistically using seine nets and hand spear while snorkelling.

Water temperature at each site in the Swan River Estuary on each sampling occasion was recorded to the nearest 0.1ºC using a Yellow Springs Instruments YSI-30 Salinity and Conductivity Metre. Mean monthly sea surface temperatures (SST) off Rottnest Island in 2008-2010 were obtained from the Reynolds SST database (Reynolds et al., 2007), which is constructed from a combination of 1) Advanced Very High Resolution Radiometer infrared satellite SST data, 2) SST data recorded from the Advanced Microwave Scanning Radiometer on the NASA Earth Observing System satellite and 3) *in situ* data from ships and buoys for 1° blocks of ocean (see Reynolds et al. (2007) for methodology). Water temperatures off Rottnest Island are similar to those in Comet Bay, the other location from which most *P. grandispinis* were collected. Mean monthly water temperatures in King George Sound were derived from daily values for November 2013 to October 2014, kindly provided by H. Patterson (University of Western Australia).

The TL of each *P. westraliae*, *P. grandispinis*, *P. laevigatus* and *L. inops* was measured to the nearest 1 mm and the total body mass of fully-intact individuals weighed to the nearest 1 g. The length-mass relationships of intact females and males of these species were calculated to estimate the mass of each fish provided as a filleted frame, but with its viscera intact, thus enabling the gondosomatic index of such fish to be estimated. The length-mass relationships of the females and males of each species were compared using

Analysis of Covariance (ANCOVA) and employing the natural logarithm of mass as the dependent variable, sex as the fixed factor and the natural logarithm of TL as the covariate.

2.2. Age validation

The techniques for ageing *P. westraliae* and *P. grandispinis*, i.e. sectioning and digital imaging of otoliths and counting of opaque zones, and for initial visual validation of ages using the trends exhibited throughout the year by marginal increments on otoliths, follow those described previously for platycephalids and other fish species (e.g. Hyndes *et al*., 1992a; Coulson *et al.*, 2014, 2016). The counts made by the senior author of the opaque zones in each sectioned otolith of these two species on three separate occasions were usually the same and, when not the case, two were always the same, and thus, in such cases, that number was recorded. The marginal increment, *i.e.* the distance between the outer edge of the single or outermost opaque zone and the otolith periphery, was expressed as a proportion of the distance between the primordium and the outer edge of the single opaque zone, when one such zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones when there were more than two or more such zones. The use of marginal increment trends to validate visually that opaque zones are formed annually in the otoliths of *P. westraliae* and *P. longipinis* was augmented by demonstrating statistically that the trends exhibited by the monthly marginal increments throughout the year conform to a single cycle (Coulson *et al*., 2016). This approach, which was based on the method described by Okamura and Semba (2009), was applied to determine the periodicity of occurrence of otoliths of each species with marginal increments falling within the lower 30 percentile of values for each category of zone counts. For this, binomial models, linked with von Mises circular distributions, were fitted assuming (1) no cycle, (2) an annual cycle or (3) a biannual cycle. The models were then compared using the Akaike Information Criterion (AIC), where the model with the smallest value was selected as best representing the data (Burnham and Anderson, 2002). Each *P. westraliae* and *P. grandispinis* was assigned an age, based on the number of opaque zones in its otoliths, the time of formation of those zones, its date of capture and a birth date of 1 January, i.e. the first day in the middle month of the spawning period of those species (see Results).

The lengths at age of *P. speculator* are taken from the data base used by Hyndes et al. (1992a), together with values for several additional fish, while the lengths at age of *P. laevigatus* and *L. inops* contain those for many extra fish beyond those employed in the analyses of Coulson et al. (2014). The opaque zones on the otoliths of these three species had previously been shown by those studies to be formed annually.

The number of opaque zones in each sectioned otolith in random subsamples of 100 otoliths of *P. westraliae* and *P. grandispinis,* which essentially encompass the ranges of numbers recorded by the first reader, was counted independently by a second experienced otolith reader (E. Ashworth). The level of precision between the two counts was assessed by calculating the average coefficient of variation (*CV*) over all fish, where

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R}\left(X_{ij} - X_j\right)^2/(R-1)}}{X_j}$$

and where, for the *j*th fish, CV_j is the age precision estimate, X_{ij} is the *i*th age determination, X_j is the mean age estimate, and *R* is the number of times each fish is aged (Chang, 1982; Campana, 2001). The resultant *CV*s of 3.8 and 2.1% for *P. westraliae* and *P. grandispinis,* respectively, demonstrate that the counts on each otolith of each species showed a high degree of agreement, falling well below the reference level of 5% for correspondence recommended by Campana (2001).

2.3. Total length and age compositions and growth

The TL and age frequency distributions of females and males of the five species in south-western Australia were plotted. Following Lek et al. (2012), the mean length and mean age of the 10% longest and 10% oldest fish of each sex of these species are considered, for statistical and comparative purposes, to reflect the maximum TLs and ages that were attained. For both the TL and age of each sex of each species, random samples of the same size as the original were drawn, with replacement, from the original sample. The mean TL and mean age of the decile of the largest and oldest fish, respectively, were calculated and stored, a process repeated, in each case, for 10 000 such samples. The means and the 2.5 and 97.5 percentiles of these 10 000 means were considered the point estimates and 95% confidence limits for fish in the uppermost deciles of their respective distributions. As in Lek et al. (2012), a randomization test was employed to compare the mean TLs and ages for fish of each sex within these uppermost deciles.

von Bertalanffy growth curves were fitted to the TLs at age for females and males of each species. The TLs at age of the smallest *P. westraliae*, *P. grandispinis* and *P. speculator*, whose sex could not be determined macroscopically, were allocated alternately to the female and male data sets used for calculating the von Bertalanffy growth curves. The von Bertalanffy growth equation is $TL = TL_{\infty}(1 - \exp[-k(t - t_0)])$, where TL is the length (mm TL) at age t (years), TL_{∞} is the mean asymptotic TL (mm) predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length. The von Bertalanffy growth equations for females and males of each species were compared using a likelihood-ratio test (Cerrato, 1990), as employed in Coulson et al. (2016).

2.4. Sex ratio and reproductive variables

The sex ratio (females : males) of each of the main TL and age classes of the five platycephalid species in south-western Australia, together with the sex ratio for all TLs and ages collectively, were calculated, but excluding the few individuals that could not be sexed. A chi-square test was used to test whether each sex ratio differed significantly from parity. Following the approach of Wenner (1972), the proportion of females in each TL class of each species, for which the sample size exceeded 10, together with 95% confidence limits, was plotted against the mid-point of the corresponding TL class for that species. A cubic smoothing spline was overlaid, ensuring that its value at each TL remained in the range of 0 to 1 by using transformed values of the proportion of females, p, employing the transformation $y = -\ln((1/p) - 1)$ and then back transforming using $p = 1/\left(1 + \exp(-y)\right)$.

When identifiable as ovary or testis, the gonads of each intact fish were removed and weighed to the nearest 0.01 g. Using criteria adapted from Laevastu (1965), these gonads were allocated to one of the following maturity stages: I-II = immature/resting; III = developing; IV = maturing; V-VI = prespawning/spawning; VII = spent and VIII = recovering spent. Although the gonads provided for 53

P. laevigatus and 40 *L. inops* were not fully intact, and could not thus be used for obtaining their masses, they could still be staged. The trends exhibited by the monthly prevalences in the different stages of ovarian development of the females of each species employed individuals whose TL ≥ their corresponding TL_{50}s at maturity.

Mean monthly gonadosomatic indices (GSIs) were determined for female and male *P. westraliae* and *P. grandispinis* with lengths ≥ their corresponding TL_{50}s at maturity (see later), using the equation GSI = W_1/W_2 x 100, where W_1 = wet gonad mass and W_2 = wet body mass. As all but four *P. laevigatus* and all *L. inops* caught during the spawning period of these two species possessed mature gonads, including the smallest female (323 mm) and male (300 mm) of the first species, the mean monthly GSIs for females and males of both species were determined using all individuals of their respective sex.

On each sampling occasion, the gonads from a subsample of *P. westraliae* and *P. grandispinis*, which encompassed a wide length range of fish and contained examples of all gonad stages found in fish in that month, were placed in Bouin's fixative for 24 to 48h, the duration depending on gonad size. The gonads were then dehydrated in a series of increasing concentrations of ethanol. The mid-region of each gonad was next embedded in paraffin wax, cut into 6 µm transverse sections, stained with Mallory's trichrome and examined using a compound microscope to validate the macroscopic staging.

The TLs at which 50 and 95% of both the females and males of *P. westraliae* and females of *P. grandispinis* attained maturity (TL_{50} and TL_{95}, respectively), together with their 95% confidence limits, were determined by logistic regression analysis, as in previous studies (Coulson *et al.*, 2005). Since essentially all of the smallest males *P. grandispinis* were mature, no attempt was made to provide a TL_{50}. Fish were considered 'mature', i.e. about to spawn, spawning or just spawned, if they possessed gonads at a stage between III and VIII. The presence of such stages, augmented by the monthly trends exhibited by the GSIs, defined the spawning period of a species and helped elucidate its peak. Logistic regression analyses for each species were restricted to data obtained during the main part of the spawning period of that species. The form of the logistic model relating the probability that a female and a male of *P. westraliae* and a female of *P. grandispinis* is mature to its TL was

$$P_{TL} = \{1 + \exp[-a(TL - TL_{50})]\}^{-1},$$

where P_{TL} is the expected proportion of mature fish at a particular TL, TL_{50} is the length at which 50% of the fish are expected to be mature, a is a (positive) parameter that determines the rate at which the proportion mature changes with length, and ln is the natural logarithm. An estimate of TL_{95} is calculated as $TL_{95} = TL_{50} + \ln(19)/a$, where TL_{95} is the length at which 95% of fish are expected to be mature. A likelihood-ratio test was used to determine whether, for *P. westraliae*, the TL_{50}s for females exceeded that of males, assuming a common value of a for each sex (Coulson *et al*., 2005).

2.5. Mortality

Estimates of instantaneous rates of natural mortality (*M*) of females and males of each of the five platycephalid species in south-western Australia were calculated from their maximum individual ages, using both the equation for fish described by Hoenig (1983) and the $\text{Hoenig}_{\text{NLS}}$ equation developed by Then et al. (2015). Note that Maunder and Piner (2015) have made the case that estimates of *M*, derived from the equation of Then et al. (2015), represent a more reliable measure than that using the equation of Hoenig (1983). The estimates of *M*, derived from the latter equation, are still provided because this equation has been widely used and therefore provides a reference point for comparisons with the results of many other studies.

The age at full recruitment for each sex of each species was considered to be represented by the age of fish that were one year older than those comprising the age class at which the frequency of individuals peaked (Ricker, 1975). Each fully-recruited age class was assigned an age relative to the age at full recruitment, with the first accorded a relative age of zero. Total mortality (*Z*) for fully-recruited fish was estimated using the Chapman and Robson (1960) approach, as implemented in the “chapmanRobson” function of the FSA Package within R (R Development Core Team, 2011; Ogle et al., 2016).

2.6. Collation of data for platycephalid species

The data for lengths, ages, growth, sex ratios and reproductive biology for platycephalid species in south-western Australia are collated, in the discussion, with those recorded for this family in the central-southern and south-eastern regions of Australia and in Japan and the Suez Canal. Where greater 'geographical' distinction within Australia is beneficial, the south-western region is regarded as comprising the Lower West Coast (LWC) between 32.0°S, 155.5°E and 32.4°S, 115.7°E and the Western South Coast (WSC) between 35.0°S, 117.4°E and 35.0°S, 117.9°E, while the south-eastern region consists of the Eastern South Coast (ESC) between 38.2°S, 144.9°E and 42.9°S, 147.8°E and the Lower East Coast (LEC) between 29.3°S, 153.2°E and 36.4°S and 150.5°E. The Central South Coast region (CSC) lies between 35°S and 123.0°E to 36°S and 134.0°E. The data for *Platycephalus caeruleopunctatus*, *Platycephalus richardsoni* and *Ratabulus diversidens* in Barnes et al. (2011) were not included because, as these authors acknowledge, the larger and potentially older individuals were under-sampled. The biological data for *Platycephalus indicus* from temperate waters of Japan (Masuda et al., 2000) and for the sex ratio and maximum TL of the females and males of *Rogadius asper* in the Suez Canal (Sabrah et al., 2015) are also included in the collated data. The data on growth and age of the latter species are not included, however, as ages were assigned by employing MULTIFAN to analyse trends exhibited by cohorts in length-frequency data, rather than by ageing of individual fish (Sabrah et al., 2015). The overall sex ratios for the species were plotted against the corresponding ratios for both the TL_∞s and maximum individual TLs of females to males.

3. Results

3.1. Water temperatures

Mean monthly water temperatures in the Swan River Estuary on the lower west coast of Australia, where *P. westraliae* was caught, rose progressively from a minimum of ~ 16ºC in mid-winter to ~ 21ºC in mid-spring and then to a maximum of ~ 25ºC in late summer and early autumn, after which they fell precipitously to ~ 17ºC in early winter (Fig. 2). Although mean water temperatures followed a similar pronounced seasonal trend in Wilson Inlet on the south coast of Western Australia, in which *P. speculator* was sampled, they peaked slightly earlier and, in each month, were between 3 and 7°C less than in the Swan

River Estuary. In marine waters on the lower west coast of Australia, along which *P. grandispinis* was collected, the mean monthly water temperatures at, for example, Rottnest Island varied far less than in the Swan River Estuary, which discharges into those coastal waters. Furthermore, unlike the Swan River Estuary, they initially declined between mid-winter and mid-spring, *i.e.* from ~ 20 to ~ 18°C, before rising to a maximum of ~ 22°C in early autumn and then remaining elevated in the ensuing three months (Fig. 2). Mean monthly water temperatures in King George Sound, one of the large embayments on the south coast of Western Australia, from which *P. laevigatus* and *L. inops* were obtained, were almost invariably higher in each month than in the nearby Wilson Inlet, but followed a similar trend throughout the year, with the minimum of 16.5°C recorded in late winter and the maximum of 21.3°C in mid-summer (Fig. 2).

3.2. Validation of ageing method

The mean monthly marginal increments on sectioned otoliths of *P. westraliae* with 2-3 opaque zones declined precipitously from typically ~ 0.59 - 0.64 in July to October to ~ 0.35 in December and January and then rose sharply and progressively to ~ 0.61 in June (Fig. 1 in Supplementary Material). This seasonal trend was also exhibited by otoliths with 1 and ≥ 4 opaque zones. Irrespective of the number of opaque zones, the mean marginal increments on sectioned otoliths of *P. grandispinis* followed the same trend as that for *P. westraliae* with 2-3 such zones and thus likewise declined to their minima around December and January, before increasing sharply in the ensuing months (Fig. 1 in Supplementary Material). The very pronounced single decline and subsequent progressive rise in mean monthly marginal increments during the year imply that a single opaque zone is formed annually in the otoliths of *P. westraliae* and *P. grandispinis*. The validity that the mean marginal increments followed a single cycle during the year is substantiated by the results of circular distribution models (Okamura and Semba, 2009; Coulson et al. 2016) and the concomitant AIC values (Table 1 in Supplementary Material). Thus, for both *P. westraliae* and *P. grandispinis*, the AIC was less for an annual cycle than no cycle or a biannual cycle for each of the two groups into which the otoliths had been pooled on the basis of the number of their opaque zones (Table 1 in Supplementary Material). Furthermore, the difference between the lowest AIC and each of the other two AICs for each group of otoliths greatly exceeded 2, the number required to identify definitively the best model in terms of the Kullback-Leibler distance (Burnham and Anderson, 2002). The number of opaque zones in sectioned otoliths can thus be used for ageing individuals of *P. westraliae* and *P. grandispinis*.

3.3. Length and age compositions and growth

The length-frequency distributions for *P. westraliae*, *P. grandispinis*, *P. speculator*, *P. laevigatus* and *L. inops* were essentially unimodal, with modal length classes for their females occurring at 300-349, 200-249, 350-399, 400-449 and 400-449 mm, respectively. The modal length class for the males of each species was similar to, or the same as, that of their females (Fig. 3). All *P. laevigatus* and the vast majority of *L. inops* were > 300 mm TL, reflecting a combination of the selectivity of the commercial gillnets used to catch these two species and the MLL of 300 mm for their retention. For all five species, the females are more abundant than males in the length classes of largest fish, among which males were frequently not represented (Fig. 3). This difference accounts for the lengths of 615, 336, 696, 552 and 655 mm for the largest females of *P. westraliae*, *P. grandispinis*, *P. speculator*, *P. laevigatus* and *L. inops*, respectively, being far greater than the corresponding lengths of 374, 276, 545, 469 and 521 mm for males. On the basis of the lengths in their upper deciles, the mean of the largest TLs of the females of each species was significantly greater ($P < 0.05$) than that of its males (Table 2 in Supplementary Material).

In terms of age, females were far more abundant than males in the two main age classes of *P. westraliae* and *P. grandispinis*, i.e. 0-4 and 5-9 years, and slightly more abundant than males in the single main age class of *P. speculator* (Fig. 3). Females were also more abundant than males in those same two age classes of *P. laevigatus* and *L. inops*, but not in subsequent age classes. The oldest females of *P. westraliae*, *P. grandispinis*, *P. speculator*, *P. laevigatus* and *L. inops* were 8, 10, 10, 25 and 20 years old, respectively, and 8, 12, 11, 22 and 17 years, respectively, with their males. On the basis of the upper deciles in ages, the mean age of the oldest females of each of the five species, except *L. inops*, was less than that of males, but the difference was significant ($P < 0.05$) only for *P. speculator* (Table 2 in Supplementary Material).

The von Bertalanffy growth curves provide visually good fits to the lengths at age of both sexes of *P. grandispinis*, *P. laevigatus* and *L. inops* and of the males of *P. westraliae* (Fig. 4). Although the curves for females of *P. westraliae* and both sexes of *P. speculator* rapidly approach their respective asymptotes, the lengths at age of the few oldest and largest fish all lie above that curve. Analysis of residuals (not shown) demonstrate, however, that distributions of deviations from the growth curves did not differ markedly from normality and that therefore, other than for the small number of lengths at age of the oldest *P. westraliae* and *P. speculator*, there were no major structural issues relating to the form of the growth curves.

Visually, the growth curves for females and males of each of the five species and between the corresponding sex in each pair of species vary markedly (all $P < 0.001$, Fig. 4, Table 1). The growth curves of both females and males in each pairwise comparison of the five species also differ markedly (all $P < 0.001$). In comparisons between the sexes of *P. westraliae*, *P. grandispinis*, *P. speculator*, *P. laevigatus* and *L. inops*, the TL_∞s for females (530, 305, 530, 504 and 615 mm, respectively) are far greater than those for males (319, 213, 450, 409 and 466 mm, respectively), whereas the values for k for females (0.41, 0.29. 0.38, 0.23 and 0.18 year^{-1}, respectively) are less than for males (0.82, 0.87, 0.48, 0.34, 0.20 year^{-1}, respectively) and markedly so for all but the last species. The above differences are reflected in an increasing divergence between the TLs of the two sexes with increasing age (Fig. 4).

3.4. Sex ratios

The percentage of females of *P. westraliae* declined from 71% at 100-149 mm TL to a minimum of 27% at 250-299 mm and then rose sharply to essentially 100% in length classes of larger fish (Fig. 5). A conspicuous rise in the percentage of females with increasing TL was also exhibited by *P. grandispinis*, *P. speculator*, *P. laevigatus* and *L. inops* (Fig. 5).

The ratios of females to males in each dominant age class of *P. westraliae* and *P. grandispinis* (0-4 and 5-9 years), and for all age classes collectively, were all ≥ 2.1:1 and the corresponding sex ratio of the overwhelmingly dominant age class (0-4 years) for *P. speculator* and overall was 1.2:1 (Table 2). Females dominated the 0-4 age classes collectively of *P. laevigatus* and *L. inops*, recognising that this age group was under-represented because samples came from the commercial fishery (Table 2). Although females were also the most abundant sex in the most dominant age class of both of these species (5-9 years), males were more numerous in the older ages collectively. The overall sex ratio favoured the females of both *P. laevigatus*, i.e. 1.3:1, and *L. inops*, i.e. 1.5:1. The sex ratio of each major age class, and overall for all species, differed from parity (typically $P < 0.001$; Table 2).

3.5. Reproductive biology

As the length-mass relationships for unfilleted females and males of *P. westraliae, P. grandispinis* and *L. inops* did not differ significantly ($P > 0.05$), the length-mass relationship for each species was calculated using the pooled data from both sexes:

$$P.\ westraliae\text{: } \ln W = 3.14 \ln TL - 12.78 \ (r^2 = 0.99, P < 0.001, n = 388),$$

$$P.\ grandispinis\text{: } \ln W = 3.30 \ln TL - 13.53 \ (r^2 = 0.97, P < 0.001, n = 561),$$

$$L.\ inops\text{: } \ln W = 3.32 \ln TL - 13.68 \ (r^2 = 0.98, P < 0.001, n = 85).$$

In contrast, the length-mass relationships for females and males of *P. laevigatus* were significantly different ($P < 0.05$) and therefore described by the following equations,

$$\text{Females: } \ln W = 3.28 \ln TL - 13.69 \ (r^2 = 0.98, P < 0.001, n = 80)$$

$$\text{Males: } \ln W = 3.19 \ln TL - 13.23 \ (r^2 = 0.98, P < 0.001, n = 51).$$

The above equations enabled the mass of each filleted fish to be estimated, which together with the mass of gonad of that fish, allowed the GSI of each filleted fish to be estimated, thereby augmenting the GSIs calculated for each whole fish. The mean monthly GSIs for female *P. westraliae* rose sharply from 1.9 in October to a well-defined maximum of 5.4 in December, and then declined precipitously to 1.6 in April and to a minimum of 0.8 in June (Fig. 6). The mean monthly GSIs for female *P. grandispinis* ≥ the TL_{50} of females, increased rapidly from 0.5 in July to 3.6 in September, after which they remained between 1.1 and 2.5 through to May. The pronounced decline in the mean GSI in October and relatively low GSIs in the immediately ensuing months is an artefact produced by an inability to obtain larger *P. grandispinis*, due to the closure to fishing of those areas where such fish were caught in other months. The mean monthly GSIs for male *P. westraliae* and male *P. grandispinis* followed the same trend as that for their females and thus likewise peaked in December and October, respectively (Fig. 6).

The mean monthly GSIs of female *P. speculator* rose sharply and consistently from ~ 0.5 in July to September to produce a conspicuous peak in December/January and then declined sequentially to ~ 0.5 in May and June, a trend followed closely by that for males (Fig. 6). The mean monthly GSI for female *P. laevigatus* increased sharply from ~ 2.0 in July to a maximum of ~ 6.0 in September and October and subsequently fell rapidly after November to ~ 0.5 in January and February, a trend again paralleled by the males (Fig. 6). The mean monthly GSI for female *L. inops* likewise followed a marked seasonal trend, but with the peak of ~ 5.8 attained slightly later, *i.e.* in November and December, a trend essentially paralleled by the values for males (Fig. 6).

All female *P. westraliae* in June to August, with TLs ≥ the TL_{50} at maturity, possessed either immature/resting (I-II) or recovering spent (VIII) ovaries, with the frequency of females possessing stage I-II ovaries declining progressively after September and remaining low or zero until March (Fig. 7). Female *P. westraliae* with ovaries at stage III (developing) and stage IV (maturing) first appeared in September and were caught in October and November. Females with stage V-VI (prespawning/spawning) ovaries were present in the eight months between October and May, dominating the samples from November to March, while those with stage VII (spent) ovaries were caught between March and August (Fig. 7). In sequential monthly samples of *P. speculator*, collected between October and March, females with stage II ovaries were rare or absent between November and March, among which months fish with ovarian stages V-VII were particularly abundant. Spent females were caught in February to April (Fig. 7). Females of *P. grandispinis* with stage I-II ovaries were almost invariably found throughout the year, while those with stages III and IV were caught exclusively between September and February, and those with stage V-VI ovaries between those two months and also from March to May, together with females with stage VII ovaries in the last three of those months.

Female *P. laevigatus* with stage I-II ovaries were rare or absent between August and December, during which months the samples of females were dominated by fish with stage V-VI ovaries (Fig. 7). Spent female *P. laevigatus* were caught between October and April. Female *L. inops* with stage I-II ovaries were caught in April and August, but not in the intervening months of September to March, with females with stage V-VI ovaries prevalent in all but the last of those months. Spent females were present between January and April (Fig. 7). In each species, recovering spent females (stage VIII ovaries) were often found towards the end or after the period when females with stage VII ovaries were caught. The trends exhibited by the prevalences of the different ovarian stages of each species are closely paralleled by those of their testes (data not shown).

During the months when female *P. westraliae* and *P. grandispinis* with ovaries at stages V-VIII became increasingly prevalent, and thus broadly represent the spawning period of those species, the females with ovaries at stages III-IV declined markedly in prevalence and, in the case of the first species, were sometimes not even represented. This implies that female *P. westraliae* and *P. grandispinis* with ovaries at stages III-IV were destined to become mature during the current spawning season and thus, together with those females with ovaries at stages V-VIII, are regarded as mature for the purposes of estimating the length (TL_{50}) and age (A_{50}) at maturity. From the GSIs and prevalences of mature females, the spawning periods mainly extend from November to March for *P. westraliae*, September to April for *P. grandispinis* and December to March for *P. speculator*.

3.6. Lengths and ages at maturity

The TLs of the smallest mature female and male caught during the spawning period of *P. westraliae* were 231 and 156 mm, respectively. During this period, maturity was attained by ~ 17% of females and males of *P. westraliae* with lengths of 200-249 and 150-199 mm, respectively, and by the vast majority of females and all males with greater lengths (Figs. 2a, b in Supplementary Material). The TL_{50} at maturity of 269 mm for the females of this species greatly exceeded the 185 mm for males ($P < 0.001$; Fig. 2 in Supplementary Material). With *P. grandispinis*, the smallest mature female and male caught during the spawning period were 151 and 132 mm, respectively. Maturity was attained by 58% of females with a TL of 150-199 mm and by essentially all of those with greater TLs, whereas the majority of males with TLs between 100 and 199 mm and all larger fish were mature (Figs. 2c, d in Supplementary Material). The TL_{50} at maturity for female *P. grandispinis* was 175 mm (Table 3 in Supplementary Material).

Although relatively few females and males of *P. westraliae* attained maturity by the end of their first year of life, the vast majority of females and all males had reached maturity by the end of their second year of life (Figs. 2e, f in Supplementary Material). The prevalence of mature females of *P. grandispinis* increased from 39% at the end of the first year of life to 75% at two years of age and to essentially 100% in all older fish, while most males became mature after only one year of life (Figs. 2g, h in Supplementary Material).

3.7. Mortality

Estimates for natural mortality (*M*) for females and males of each of the five species were greater when using the equation of Then et al. (2015) than that of Hoenig (1983) (Table 3), noting that, through cross validation, Then et al. (2015) demonstrated that their equation provided a better estimate than others used to predict published values of *M*. The catch curve estimates of total mortality (*Z*) for both sexes of each of the five species, except for those of *P. speculator*, were similar or slightly less than the corresponding estimates of *M* derived from the equation of Then et al. (2015). Point estimates of *Z* for both sexes of *P. speculator* greatly exceed the corresponding estimates of *M*, recognising that the estimate of *Z* for females was less precise than those for *Z* for either sex of the other four species (Table 3).

4. Discussion

This review has produced an integrated account of the extent to which biological characteristics, such as the length and age compositions, growth and reproductive biology, vary among species within a family of fishes, with a focus on factors affecting the sex ratio. The data recorded and collated during the study (Table 4) represent nine of the 11 species of Platycephalidae reported by Gomon et al. (2008) for the very extensive southern Australian coast, which is at the centre of the temperate region at the lower limits of the Indo-west Pacific region. Furthermore, the species include eight of the *Platycephalus* genus listed in

Gomon et al. (2008) and also *Platycephalus westraliae*, an essentially tropical species which, in south-western Australia, is confined to the Swan River Estuary (Potter et al., 1990). Two species, *Platycephalus laevigatus* and *Platycephalus grandispinis*, were represented by populations in both south-western and south-eastern Australia.

In the collated list, *Leviprora inops* was one of only two platycephalid species from a genus other than *Platycephalus*, recorded by Gomon et al. (2008) for the southern Australian coast. Data are also included for *Ambiserrula jugosa*, recognising that this essentially tropical platycephalid (Paxton et al., 2008) extends only as far south as Botany Bay at ~ 34°S on the east coast of Australia, together with the only comprehensive published data for a gonochoristic platycephalid elsewhere, i.e. those for *Platycephalus indicus* from temperate waters in Japan (Masuda et al., 2000). Note that, although differing in genus and/or region, the trends exhibited by the biological characteristics of *L. inops*, *A. jugosa* and *P. indicus* are consistent with those for other platycephalid species in southern Australia (Table 4) and the same is true for the more limited information for *Ratabulus diversidens* from the Gulf of Suez. The data for two protandric hermaphroditic species in Japan (Fujii, 1970, 1971; Shinomiya et al., 2003) were not included since the present review focused on dioecious species. In particular, analyses of the extents to which the sex ratios of species within the Platycephalidae change with body size and are related to the magnitude of the differences in the TL_∞s and maximum TLs of the two sexes were determined, the first time that such relationships for a family or genera of fishes have been examined statistically.

4.1. Estuarine mode of life of Platycephalus westraliae and *Platycephalus speculator*

The prevalences of each sequential stage in ovarian development of *P. westraliae* in the Swan River Estuary and *P. speculator* in Wilson Inlet were shown to change progressively throughout the year as the gonads develop towards spawning condition and eventually become spent (Fig. 7). The continuity in this process is emphasised by each of those stages of each species being abundant at the appropriate time of the reproductive cycle and their larvae being present in the main body of those systems at the time when those species spawn (Neira et al., 1992; Neira and Potter, 1992). The above trends provide overwhelming evidence that at least the majority of the individuals of *P. westraliae* in the Swan River Estuary and of *P. speculator* in the Wilson Inlet complete their life cycles in those systems. This conclusion is further endorsed by the fact that *P. speculator* spawned in Wilson inlet in a year in which that estuary was closed from the sea at the time of spawning (Hyndes et al., 1992b).

Since, during their spawning seasons, essentially all females of *P. westraliae* and *P. speculator* are mature by the time they are two years old and many individuals reach seven years old, with some of the latter attaining appreciably older ages, both species spawn in their respective estuaries during several successive annual spawning seasons.

Although *P. westraliae* is abundant in the Swan River Estuary, it is not common in coastal waters on the lower west coast of Australia and even then is found only in waters highly or moderately sheltered from wave activity and with seagrass present or nearby (Valesini et al., 2004). This species is present, however, in the large marine embayment of Shark Bay much further north, where there are no estuaries (Travers and Potter, 2002). The restriction of the essentially tropical *P. westraliae* largely to estuaries in the extreme southern part of their distribution and their presence in Shark Bay parallels the situation described for *Amniataba caudivittata* (Lenanton, 1977; Potter et al., 1994b).

Platycephalus speculator is abundant not only in Wilson Inlet, but also other south coast estuaries such as the Nornalup-Walpole Estuary (Potter and Hyndes, 1994) and in the large protected and relatively nearby embayments of King George Sound and Princess Royal Harbour (P. Coulson, pers. comm.). In contrast, apart from in a few small areas that provide protection, *P. speculator* is not abundant in marine waters along this exposed coast (Ayvazian and Hyndes, 1995; P. Coulson, pers. observ.). The possibility that some of the individuals in coastal marine may have resulted from flushing out from the estuary cannot be excluded. In contrast, on the lower west coast, which is protected by a line of limestone reefs, *P. speculator* acts as a typical marine estuarine-opportunist species sensu Potter et al. (2015) by using estuaries mainly as a nursery area and not for spawning (Potter and Hyndes, 1999). It is thus proposed that, on the exposed south coast, there were strong selection pressures for *P. speculator* to complete the whole of its life cycle in the protected waters of estuaries and embayments, whereas such selection pressures were not pronounced on the protected lower west coast.

4.2. Maximum total lengths and ages and growth

The results of statistical analyses, using the uppermost deciles of the TLs and ages of the females and males of *P. westraliae*, *P. grandispinis, P. speculator*, *P. laevigatus* and *L. inops* in south-western Australia, are consistent with the following hypotheses. The females of each of these species grew to a significantly greater TL than males, whereas, except for *L. inops,* the males of those species attained a greater age than females, but this difference was significant only with *P. speculator*. The extent of sexual dimorphism in TL of the five species in south-western Australia varies appreciably, with the difference between the mean TLs of the largest individuals of the two sexes ranging from 1.1 times for *P. speculator* to 1.6 times for *P. westraliae*. The contrast between the significant differences in TL attained by the two sexes and a tendency for a reverse trend by their ages is reflected in the von Bertalanffy growth curves of the females and males of each of the five species differing significantly, with the TL_∞s far greater for females than males.

The above relationships between the TLs and ages of each sex for platycephalids in south-western Australia are paralleled by those in a population of *P. laevigatus,* two populations of *P. grandispinis* and five other platycephalid species from much further east in the central-southern and south-eastern regions of Australia. Thus, the maximum individual TLs and TL_∞s of those species were greater for females than males and there was no consistent overall trend for the maximum individual ages of those species to be greater for either sex across those populations (Table 4). Although the ratio of 2.9 for the TL_∞ of the females (1275 mm) to males of *P. fuscus* (432 mm) far exceeded that of any other platycephalid species (Fig. 8a), the difference was far less pronounced for the ratio of 1.6 for the maximum individual TLs of females (985 mm) to males (615 mm), with that ratio lying within the range of other platycephalids (Fig. 8b). The apparently anomalous very high ratio for TL_∞s for the two sexes of *P. fuscus* is related to the TL_∞ for females being far greater than the maximum individual TL, whereas the reverse is markedly the case for males (see Fig. 6 in Gray and Barnes, 2015). For this reason, the TL_∞s for *P. fuscus* were not included in Fig. 8a.

The length compositions of both sexes vary markedly among platycephalid species, with maximum individual TLs ranging from 221 and 206 mm for females and males of *A. jugosa* to 985 and 615 mm for males of *P. fuscus* (Table 4). As with maximum TLs, the TL_∞s range widely from, for example, 251 mm for females in one of the populations of *P. grandispinis* to 1275 mm for *P.fuscus* (Tables 1, 4), emphasising that the patterns of growth of particularly the females of the various platycephalid species differ greatly (Fig. 9). The maximum individual ages also varied markedly among species, with maxima of 26 years for a female *P. conatus* from the central- southern coast and 25 years for a female *P. laevigatus* from the south-western coast, which only slightly exceed the maxima of 23 years for a male *P. bassensis* from the south-eastern coast and 22 years for a male *P. laevigatus* on the south-western coast (Table 4). In contrast, maximum individual ages of only eight years were recorded for both sexes of *P. westraliae* on the south-western coast and even lower values of four years for both the females and males of *A. jugosa*.

The early growth of the females and males of *P. westraliae* in the Swan River Estuary in south-western Australia is greater than that of the corresponding sex of *P. grandispinis* in coastal waters in the immediate vicinity of the Swan River Estuary. This is illustrated by predictions from the von Bertalanffy growth curves, that, for example, the females of *P. westraliae* at two and three years of age reach 300 and 377 mm, respectively, compared with only 198 and 225 mm, respectively, for *P. grandispinis,* a trend paralleled by the predictions for the males of those two species. The corresponding values for females of *P. speculator* at the same ages, i.e. 339 and 403, respectively, were even greater than those of *P. westraliae* and thus far exceed those of *P. grandispinis*.

The substantial size attained early in life by *P. westraliae* in the Swan River Estuary and *P. speculator* in Wilson Inlet, in which they typically complete their life cycles, is consistent with the view that the exceptionally high productivity of estuaries (Schelske and Odum, 1961; Contanza et al., 2007; Houde and Rutherford, 1993) facilitates particularly rapid growth of juvenile fish (Blaber and Blaber, 1980; Le Pape et al., 2003; Yamashita et al., 2003; Veale et al., 2016). The greater productivity of estuaries than coastal waters is exemplified by nematodes and benthic macroinvertebrates, which are important components of food chains in these waters (Platell et al., 2006; French et al., 2013; Coulson et al., 2015;

Tweedley et al., 2016), having far greater densities in the Swan River Estuary than in nearby coastal waters where *P. grandispinis* lives (Wildsmith et al., 2005, 2011; Hourston et al., 2011), the latter trend paralleling those found in corresponding environments in the Northern Hemisphere (e.g. Tweedley et al., 2015). The pronounced similarity in the growth curves of the females of *P. speculator* and *P. westraliae* is particularly striking since the diets of these two species differ markedly, with the former feeding predominantly on carid crustaceans throughout life, whereas the latter feeds mainly on a range of invertebrates when small and on teleosts when large (Coulson et al., 2015). Furthermore, as the early growth of *P. fuscus* was even more rapid than in *P. westraliae* and *P. speculator* and all other species elsewhere in Australia, it is relevant that this platycephalid spends at least much of its life in estuaries (Pollock, 2014; Gray and Barnes, 2015).

Although the paucity of data for young *P. laevigatus* and *L. inops* in south-western Australia necessitates caution in extrapolating from the data for the lower ends of the von Bertalanffy growth curves for these two species, those curves still imply that the early growth of those species is also rapid. As the embayments, in which those species were caught, are largely enclosed and contain very extensive seagrass meadows, the habitat of *P. laevigatus* and *L. inops*, the morphological and productivity characteristics of those embayments are similar to those of the nearby Wilson Inlet (Hutchings et al., 1991; Kirkman et al., 1991), thereby playing a similar role to estuaries in facilitating rapid growth.

4.3. Sex ratios

It was particularly striking that, after individuals of the five platycephalid species in south-western Australian had reached a certain size, the proportion of females subsequently rose progressively with increasing TL, eventually approaching or reaching 100%. This trend is due to females growing more rapidly than males and thus to their representation by lower numbers than males at intermediate TLs but by greater numbers among the larger fish. The possibility that sequential changes in sex ratio with length may also be largely attributable to differential total mortality (Z) of the females and males of *P. laevigatus* and *L. inops* is unlikely on the grounds that the estimates of Z for the two sexes of those species are very similar (Table 3). Furthermore, estimates of Z for *P. westraliae*, *P. grandispinis* and *P. speculator* are rather greater for females than males, which is contrary to the trend that would lead to an increasing percentage of females as fish became older. The trend for the ratio of females to males in the five south-western Australian species to rise markedly, after attaining a particular body size, parallels that recorded by Cerviño (2014) for the European Hake *Merluccius merluccius* in the Bay of Biscay. That author regarded this trend to be due to differences in mortality as well as growth of the two sexes.

In marked contrast to the trend for the sex ratio of each of the five species to change progressively with TL, after a particular length had been attained, there was no pronounced trend for sex ratio change with age, with the females dominating the abundant age classes of each of the five species. While, on the basis of their upper deciles, the TLs were significantly greater for females than males for each of the five species in south-western Australia, the ages were greater for the males than females of four of those species, with the difference being significant, however, with only one of those species. The above trends imply that the greater proportion of females than males cannot be attributed to a greater longevity of females. This finding contrasts with the implications of several other studies, including those on another ‘flatfish’ species, the Summer Flounder *Paralichthys dentatus* from the Atlantic Ocean (Maunder and Wong, 2011), and on the Vermillion Snapper *Rhomboplites aurorubens* in Northern and Southern Carolina (Grimes and Huntsman, 1980), that a dominance of females of those species was due to a greater longevity of that sex. The possibility that sex reversal (i.e. hermaphroditism) could account for the excess of females in the five platycephalid species from south-western Australia is excluded as histological studies showed that the gonads of these species contained exclusively either ovarian or testicular tissue (P. Coulson unpublished data) and because their females almost invariably predominated in the major age classes of each species. As the ratio of females to males significantly exceeded parity (all $P < 0.001$) in all fish species outside the spawning period and in three of those species during the spawning period and did not exceed parity in the other two species, it seems unlikely that the overall predominance of females in those five species is due to pronounced differential, spawning-related migratory patterns of the two sexes. This further enhances the conclusion that greater growth by females is the major factor contributing to the greater abundance of females than males of gonochoristic species of the Platycephalidae.

The wide range in overall ratios of females to males for the five species in south-western Australia, i.e. 1.2:1 for *P. speculator* to 2.7:1 for *P. westraliae*, falls within the range of the ratios for the composite data for all platycephalid species, which extend from close to parity for two populations of *P. bassensis* and a population of *P. laevigatus* in south-eastern Australia and a population of *P. indicus* from Japan to as high as 3.2:1 for populations of *P. conatus* and *P. fuscus* from central-southern and south-eastern Australia, respectively (Figs 8a, b).

The overall sex ratio of females (SR) to males was positively related to the ratios of both the (a) TL_∞s and (b) maximum TLs ($TL_{\max}$) of the females to males (Fig. 8a, b), as described by the following equations:

$$\text{a) } \ln\text{SR} = 1.99(\ln TL_\infty) - 0.03 \ (r^2 = 0.56, P < 0.01, n = 15),$$

$$\text{b) } \ln\text{SR} = 2.21(\ln TL_{\max}) - 0.005 \ (r^2 = 0.57, P < 0.01, n = 16).$$

The combination, in three species, of a very high overall ratio of females to males and a particularly large maximum size of females, at least with respect to their males (Fig. 8b), probably reflects strong selection pressures for maximising the overall production of young of those species. It may thus be relevant that the greatest difference between the maximum size of the females and males was exhibited by two of the three species found in estuaries, i.e. *P. fuscus* and *P. westraliae*, and that this was allied with a very high ratio of females to males. The optimisation of the production of young by these species would help offset the potential susceptibility for their small individuals to be swept out of the estuary during their first winter of life as freshwater discharge increases due to high winter rainfall. The third species of estuarine resident, *P. speculator*, would not be faced, to the same extent, with such potential problems as it lives in an estuary that typically remains closed until spring, when discharge becomes sufficient to help breach the bar at the mouth of this estuary, by which time the youngest fish have reached a larger size than their counterparts in *P. fuscus* and *P. westraliae* in winter. The third large species, *P. conatus*, whose females are far larger and in much greater abundance than their males, is found further offshore and in deeper oceanic waters than other platycephalid species (Stokie and Talman, 2003; Brown and Sivakumaran, 2007; Gomon et al., 2008). The very substantial sexual dimorphism in body size of this particularly large platycephalid is consistent with the demonstration by Rijnsdorp et al. (2015) that the degree of such sexual dimorphism among marine flatfish species in European waters is related to the body size attained by those species, a feature they attributed to natural mortality in the ocean being strongly related to body size.

4.4. Gonadal maturation and spawning period

The trends exhibited by the prevalences of the various gonad stages and GSIs in sequential months demonstrate that the spawning periods of the five platycephalid species in south-western Australia overlap (Fig. 10). The timing of the commencement of spawning formed a sequence, however, from early spring with *P. laevigatus* and *L. inops* to mid-spring with *P. grandispinis* to late spring with *P. westraliae* to early summer with *P. speculator*. Spawning was thus initiated as temperatures had troughed with *P. grandispinis* and were increasing with the other four species. While the trend for these species to spawn when temperature is increasing is typical for teleosts in temperate environments (Lam, 1983), the above interspecific differences in timing imply that the ‘sensitivity’ of endocrine and other internal processes responsible for initiating spawning varies among species. It is also relevant that *P. westraliae* and *P. speculator*, which commence spawning relatively late compared with the overall trend, i.e. November and December, respectively, and after temperatures have been increasing for some months, spend their whole life cycle in estuaries. A delay in spawning by these species until late spring and early summer results in it occurring after freshwater discharge has declined markedly and salinities are relatively high and stable, due to the majority of precipitation in south-western Australia occurring in winter (Cottingham et al., 2016). Thus, spawning takes place when conditions are relatively stable and benign and conducive to successful spawning and retention of larvae (Potter and Hyndes, 1999). The commencement of spawning of *P. fuscus* in the lower reaches of estuaries in eastern Australia also occurs relatively late (Fig. 10).

The data on the prevalence of immature and mature *P. westraliae* and *P. grandispinis* in south-western Australia clearly demonstrate that the females of both of these species reach maturity at significantly greater TLs than their males. On the other hand, the females and males of *P. westraliae* attain maturity at similar ages, i.e. occurring with a few individuals of both sexes at the end of their first year of life and by essentially all fish by the end of their second year of life. Although a similar trend was exhibited by *P. grandispinis* in south-western Australia, a greater proportion of individuals, and particularly of males, reached maturity at the end of their first year of life, as is the case with *P. speculator* in Wilson Inlet (Hyndes et al., 1992b). The TL_{50}s for the two sexes for the only four other platycephalid species elsewhere, for which there are such data, demonstrate that, as with the above three species in south-western Australia, the females attain maturity at a greater TL than their males, with the difference particularly pronounced with *P. fuscus*, i.e. 567 vs 367 mm (Table 4). Although the age at maturity of the females of *P. fuscus* also exceeded that of its males, i.e. 4.5 vs 1.2 years, the ages at maturity of the females and males of the other two species, for which there were data, were similar in the case of *P. laevigatus* and the same for *P. bassensis* (Table 4).

4.5. Mortality

The direct estimates of total mortality (*Z*) for female and male *P. grandispinis*, *P. westraliae*, *P. laevigatus* and *L. inops*, derived from catch curve analysis, must exceed the true value of natural mortality (*M*). As the indirect estimates of *M* for these species, derived from the equation of Then et al. (2015), exceed, to a certain degree, the estimates of *Z*, they are considered overestimates. However, the indirect estimates of *M* for these four species, derived using the equation of Hoenig (1983), are typically rather less than the corresponding values for *Z* and thus apparently provide, for these species, estimates of *M* that are more consistent with those of *Z*. The fact that the values for *Z* do not differ markedly from those of *M* from the Hoenig (1983) equation is consistent with the, at best, limited extent to which those species are fished. Thus, *P. westraliae* is fished only lightly by recreational fishers in the Swan River Estuary and, in the period of sampling, by only three commercial fishers, who did not target that species, and the TLs of the vast majority of *P. grandispinis* are less than the minimum legal length of 300 mm for platycephalids in Western Australia and are thus discarded when caught. Furthermore, *P. laevigatus* and *L. inops* are not targeted and form only small components of the catches of a multispecies fishery (Smith et al., 2015).

The far higher estimate of *Z* than *M* for both sexes of *P. speculator* in Wilson Inlet suggests that this species was substantially exploited in that system in the years immediately prior to when the samples of this platycephalid were collected. It is relevant that any fished species, such as *P. speculator*, which completes its life cycle within Wilson Inlet (Hyndes et al., 1992a, b), would be susceptible to the effects of fishing, especially as this system contains the largest estuarine commercial fishery in Western Australia. In this context, it is noteworthy that the Estuary Cobbler *Cnidoglanis macrocephalus*, which likewise completes its life cycle in Wilson Inlet (Laurenson et al., 1993, 1994), has been shown to have experienced heavy exploitation in that estuary (Chuwen et al., 2011).

5. Conclusion

In summary, the results derived and collated during the present study demonstrate that the growth and longevity of the temperate gonochoristic species of Platycephalidae vary markedly. In addition, the extent of differences in the growth of females and males of a species, as reflected by their maximum TLs and TL_∞s, also varies markedly among species. Furthermore, the sex ratios, which range widely from parity to 3.2:1, were positively correlated with the extents to which both the TL_∞ and maximum TL of females exceed those of males. These and estimates of mortality and the lengths and ages at maturity of the two sexes strongly indicate that sex ratio differences and attainment of maturity are related to growth rather than longevity. It is proposed that species with a high female to male sex ratio and far greater body size of females than their males have been subjected to selection pressures for maximising the production of young. Early growth is rapid in the three species occupying estuaries, presumably reflecting the high productivity of these systems. The spawning period of the various species ranges progressively from those in which it commences in early spring, as temperatures had fallen to their minima, to those in which it starts in late spring/early summer and thus after temperatures have been rising for some time. Since the species found in estuaries fall in the last category, their individuals would benefit from spawning at a time when salinities and temperatures are high and relatively stable and fresh water discharge, and thus turbulence, is low, thereby providing a benign environment ideal for spawning success and larval retention.

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List of Figures

Fig. 1. Map showing a) locations in Western Australia of the Swan River Estuary (SRE) on the lower west coast and of Wilson Inlet (WI) and Princes Royal Harbour (PRH) on the south coast, and details of b) Swan River Estuary in which *Platycephalus westraliae* was sampled, c) Rottnest Island, Cockburn Sound and Comet Bay from which *Platycephalus grandispinis* was obtained, and d) Wilson Inlet where *Platycephalus speculator* was collected by Hyndes et al. (1992a, b) and Princess Royal Harbour and King George Sound in which *Platycephalus laevigatus* and *Leviprora inops* were sampled.

Fig. 2. Mean monthly water temperatures ± 1 S.E. at sites sampled in the Swan River Estuary (white circles, solid line) and in coastal waters southwards along the lower west coast of Australia (grey circles, dashed line) and in Wilson Inlet (white circles, dotted line) and King George Sound (black circles, solid line) on the south coast.

Fig. 3. Length-frequency and age-frequency distributions for females (black bars) and males (grey bars) of *Platycephalus westraliae*, *Platycephalus grandispinis*, *Platycephalus speculator*, *Platycephalus laevigatus* and *Leviprora inops.* White bars denote the small fish whose sex could not be determined macroscopically.

Fig. 4. von Bertalanffy growth curves fitted to the lengths at age of females and males of *Platycephalus westraliae*, *Platycephalus grandispinis*, *Platycephalus speculator*, *Platycephalus laevigatus* and *Leviprora inops* The lengths of the small *P. westraliae* and *P. grandispinis* that could not be sexed were assigned alternately to the female and male data sets.

Fig. 5. The percentage of females, and 95% confidence interval, in each abundant length class of *Platycephalus westraliae*, *Platycephalus grandispinis*, *Platycephalus speculator*, *Platycephalus laevigatus* and *Leviprora inops*, overlaid with a cubic smoothing spline.

Fig. 6. Mean monthly gonadosomatic indices ± 1 S.E. for females and males of *Platycephalus westraliae, Platycephalus grandispinis, Platycephalus speculator, Platycephalus laevigatus* and *Levipora inops*. Closed rectangles on x-axis refer to winter and summer months and open rectangles to spring and autumn months.

Fig. 7. Monthly percentage frequencies of occurrence of sequential stages in gonadal development of females and males of *Platycephalus westraliae*, *Platycephalus grandispinis*, *Platycephalus laevigatus* and *Levipora inops* ≥ their TL_{50} at maturity and of *Platycephalus speculator* ≥ 2 years old. Histograms for stages V and VI collectively are highlighted in black. Data on gonadal stages of females and males of *P. speculato*r came from Hyndes et al. (1992b), in which data for the months between May and September were pooled. Closed rectangles on x-axis refer to winter and summer months and open rectangles to spring and autumn months.

Fig. 8. Relationships between the sex ratio (females to males) and (a) ratio of TL_∞s of females to males and (b) ratio of maximum TLs of females to males for the species and populations in Table 4, and for TL_{max} for *Rogardus asper*. Note that, *Platycephalus fuscus* was not included in a) as the TL_∞s for the females and males were anomalous (see Discussion for rationale). Numbers after species refer to references given as footnotes in Table 4. In this Fig. and Fig. 9, a refers to studies on lower west and western south coasts; b to central southern coast; c to eastern south coast and d to lower east coast. * denotes that the species is represented by more than one population on the same coast.

Fig. 9. Comparisons of von Bertalanffy growth curves fitted to the lengths at age of females and males of *Platycephalus* species from Australian and Japanese waters. Numbers after species refer to references given as footnotes in Table 4. The von Bertalanffy growth curve for female *P. laevigatus* from the eastern south coast is not shown as it essentially coincides with that for this species on the western south coast.

Fig. 10. Spawning periods of gonochoristic platycephalid species from Australian and Japanese waters. The spawning period for *Platycephalus indicus* is shown according to the austral calendar. WSC, western south coast; CSC, central southern coast; ESC, eastern southern coast; LEC, lower east coast. Numbers after species refer to references given as footnotes in Table 4. * denotes that the species is represented by more than one population on the same coast.

Supplementary Fig. 1. Mean monthly marginal increments ± 1 SE on sectioned sagittal otoliths of *Platycephalus westraliae* and *Platycephalus grandispinis* with different numbers of opaque zones. Sample sizes are shown above each mean. Closed rectangles on x-axis refer to winter and summer months and open rectangles to spring and autumn months.

Supplementary Fig. 2. Percentage frequency of occurrence of females and males of *Platycephalus westraliae* and *Platycephalus grandispinis* with gonads at stages III-VIII (grey histograms) in sequential a) 50 mm length classes and b) at 1, 2, 3 years etc. Data were derived from fish caught during the main part of the spawning periods of those species, i.e. November to March and December to March, respectively. In a), logistic curves (solid lines) and their 95% confidence limits (dotted line) were fitted to the probability that a fish at a specific TL was mature. Sample sizes are shown at top of each histogram.

Table 1. The von Bertalanffy growth curve parameters TL_∞, k and t_0, and their upper and lower 95% confidence limits, for the females and males of the five abundant platycephalid species in south-western Australia. Parameters were derived from the TLs at age of individuals. r^2 = coefficient of determination; n = sample size.

		von Bertalanffy parameters				
		TL_∞ (mm)	**k (year^{-1})**	**t_0 (years)**	**r^2**	***n***
Platycephalus westraliae						
Female	**Estimate**	**530**	**0.41**	**-0.04**	**0.76**	**384**
	Upper	557	0.48	0.14		
	Lower	502	0.34	-0.22		
Male	**Estimate**	**319**	**0.82**	**0.05**	**0.88**	**150**
	Upper	327	0.95	0.15		
	Lower	310	0.71	-0.05		
Platycephalus grandispinis						
Female	**Estimate**	**305**	**0.29**	**-1.54**	**0.77**	**387**
	Upper	319	0.35	-1.12		
	Lower	292	0.24	-1.96		
Male	**Estimate**	**213**	**0.87**	**-0.28**	**0.61**	**181**
	Upper	220	1.10	0.06		
	Lower	207	0.64	-0.62		
Platycephalus speculator						
Female	**Estimate**	**530**	**0.38**	**-0.42**	**0.69**	**796**
	Upper	563	0.45	-0.22		
	Lower	499	0.31	-0.62		
Male	**Estimate**	**450**	**0.48**	**-0.16**	**0.74**	**682**
	Upper	466	0.54	-0.02		
	Lower	434	0.42	-0.31		
Platycephalus laevigatus						
Female	**Estimate**	**504**	**0.23**	**-1.86**	**0.73**	**434**
	Upper	513	0.26	-1.31		
	Lower	495	0.20	-2.41		
Male	**Estimate**	**409**	**0.34**	**-1.26**	**0.62**	**322**
	Upper	414	0.38	-0.79		
	Lower	404	0.29	-1.74		
Leviprora inops						
Female	**Estimate**	**615**	**0.18**	**-1.37**	**0.79**	**241**
	Upper	739	0.21	-0.76		
	Lower	591	0.15	-1.98		
Male	**Estimate**	**466**	**0.20**	**-1.59**	**0.76**	**164**
	Upper	485	0.24	-0.82		
	Lower	446	0.16	-2.36		

Table 2. Ratio of females to males in each age class and overall of the five abundant platycephalid species in south-western Australia and also their associated chi-square (χ^2) values and significance levels (*P*) when represented by a sample of at least 50 fish. *n*, sample size

Species	**Age class**	**Sex ratio**	χ^2	***P***	***n***
Platycephalus westraliae	0-4	2.9:1	97.8	<0.001	405
	5-9	2.1:1	178.7	<0.001	101
	overall	2.7:1	109.1	<0.001	506
Platycephalus grandispinis	0-4	2.1:1	60.1	<0.001	475
	5-9	2.7:1	18.6	<0.001	86
	10-14	0.4:1			7
	overall	2.1:1	72.8	<0.001	568
Platycephalus speculator	0-4	1.2:1	14.6	<0.001	1399
	5-9	0.2:1			44
	10-14	0.3:1			4
	overall	1.2:1	8.98	<0.01	1447
Platycephalus laevigatus	0-4	2.3:1	13.8	<0.001	94
	5-9	1.5:1	19.6	<0.001	432
	10-14	0.9:1	0.21	0.64	170
	15-19	0.9:1			40
	20-24	0.1:1			9
	overall	1.3:1	17.6	<0.001	745
Leviprora inops	0-4	3.5:1	17.6	<0.001	58
	5-9	1.6:1	15.1	<0.001	247
	10-14	0.5:1	7.45	<0.05	71
	15-19	1.6:1			16
	overall	1.5:1	14.6	<0.001	392

Table 3. Maximum age, peak in age composition and estimates of natural mortality (M) for females and males of the five abundant platycephalid species in south-western Australia, calculated using the Hoenig (1983) (M^1) and Then et al. (2015) (M^2) equations, and estimates of total mortality (Z and SE year^{-1}) calculated using the catch curve method of Chapman and Robson (1960).

		Max. age	Peak age	M^1	M^2	Z (SE)
Platycephalus westraliae	Females	8	3	0.53	0.73	0.60 (0.18)
	Males	8	3	0.53	0.73	0.41 (0.12)
Platycephalus grandispinis	Females	10	3	0.42	0.59	0.49 (0.05)
	Males	12	3	0.35	0.50	0.32 (0.05)
Platycephalus speculator	Females	10	4	0.42	0.59	1.48 (0.64)
	Males	11	4	0.38	0.54	1.09 (0.17)
Platycephalus laevigatus	Females	25	6	0.17	0.26	0.28 (0.03)
	Males	22	7	0.19	0.29	0.23 (0.04)
Leviprora inops	Females	20	6	0.21	0.31	0.30 (0.04)
	Males	17	7	0.25	0.37	0.32 (0.06)

Table 4. The von Bertalanffy growth curve parameters L_∞, k and t_0, length and age at maturity (L_{50} and A_{50}, respectively), maximum age and maximum total length (TL) for the females and males of platycephalid species. LWC, lower west coast; WSC, western south coast; CSC, central south coast; ESC, eastern south coast; LEC, lower east coast.

		TL_∞	k	t_0	TL_{50}	A_{50}	Max. age	Max. TL
Females								
Platycephalus westraliae[1]	LWC	530	0.41	-0.04	259	2	8	615
Platycephalus grandispinis[1]	LWC	305	0.29	-1.54	172	2	10	336
Platycephalus grandispinis[2]	LEC	251	0.46	-1.18			12	262
Platycephalus grandispinis[2]	LEC	311	0.44	-1.26			13	311
Platycephalus speculator[1,3]	WSC	530	0.38	-0.42	340	2	10	696
Platycephalus laevigatus[1]	WSC	504	0.23	-1.86			25	552
Platycephalus laevigatus[4]	ESC	547	0.17	-2.14	264	1.4	21	540
Leviprora inops [1]	WSC	615	0.18	-1.37			20	655
Platycephalus bassensis[4]	ESC	277	0.46	-1.38			23	370
Platycephalus bassensis[5]	ESC	404	0.23	-0.52	235	3	16	475
Platycephalus conatus[6,7]	CSC	717	0.18	-0.82	400	3.8	26	820
Platycephalus fuscus[8]	LEC	1275	0.08	-2.39	567	4.5	16	985
Platycephalus richardsoni[9]	LEC	766	0.12	-0.65	360		12	650
Platycephalus aurimaculatus[10]	ESC	545	0.33	-0.06			16	595
Ambiserrula jugosa[2]	LEC	292	0.20	-1.30			4	221
Platycephalus indicus[11]	Japan	430	0.67	-0.09			12	635
Males								
Platycephalus westraliae[1]	LWC	319	0.82	0.05	187	2	8	374
Platycephalus grandispinis[1]	LWC	213	0.87	-0.28	100	1	12	276
Platycephalus grandispinis[2]	LEC	231	0.53	-1.18			16	253
Platycephalus grandispinis[2]	LEC	241	0.52	-1.18			12	262
Platycephalus speculator[1,3]	WSC	450	0.48	-0.16	200	1	11	545
Platycephalus laevigatus[1]	WSC	409	0.34	-1.26			22	469
Platycephalus laevigatus[4]	ESC	520	0.10	-5.79	231	1.8	16	426
Leviprora inops [1]	WSC	466	0.20	-1.59			17	521
Platycephalus bassensis[4]	ESC	260	0.27	-3.79			23	334
Platycephalus bassensis[5]	ESC	366	0.22	-0.79	210	3	17	427
Platycephalus conatus[6]	CSC	494	0.35	-0.37			19	590
Platycephalus fuscus[8]	LEC	432	0.71	-0.67	317	1.2	11	615
Platycephalus richardsoni[9]	LEC	589	0.18	0.63	300		10	490
Platycephalus aurimaculatus[10]	ESC	485	0.17	-2.53			18	509
Ambiserrula jugosa[2]	LEC	211	0.31	-1.30			4	206
Platycephalus indicus[11]	Japan	551	0.48	-0.12			16	476

Numbers after species in this Table and Figs 7, 8 and 9 refer to following references: [1]Present study; [2]Barnes et al. (2011); [3]Hyndes *et al.* (1992a, b); [4]Koopman et al. (2004); [5]Jordan (1998, 2001); [6]Stokie and Talman (2003); [7]Brown and Sivakumaran (2007); [8]Gray and Barnes (2015); [9]Montgomery (1985); [10]Cottier (1999); [11]Masuda et al. (2000); [12]Pollock (2014); [13]Sabrah et al. (2015).

Supplementary Table 1. Akaike Information Criterion values, for otoliths of *Platycephalus westraliae* and *Platycephalus grandispinis* with marginal increments falling within the lower 30 percentile of values for each category of zone counts, determined by binomial circular distribution models fitted assuming no cycle, an annual cycle and a biannual cycle. Values in bold text are the smallest, which the associated models selected as best representing the data.

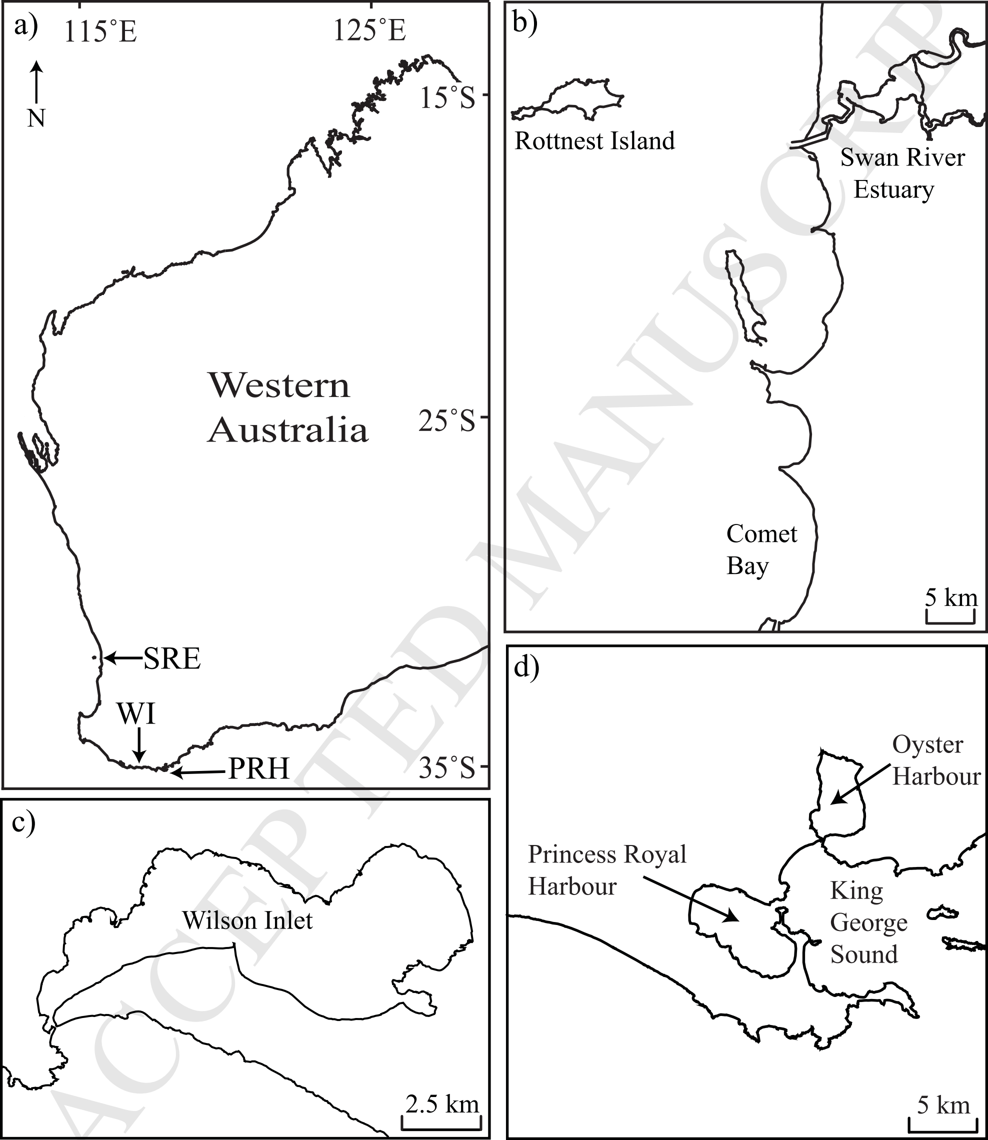
		1 zone	2-3 zones	≥ 4 zones
Platycephalus westraliae	No cycle	41	248	264
	Annual cycle	**21**	**196**	**176**
	Biannual cycle	39	232	225
		1 zone	2 zones	≥ 3 zones
Platycephalus grandispinis	No cycle	151	248	244
	Annual cycle	**120**	**174**	**204**
	Biannual cycle	127	211	243

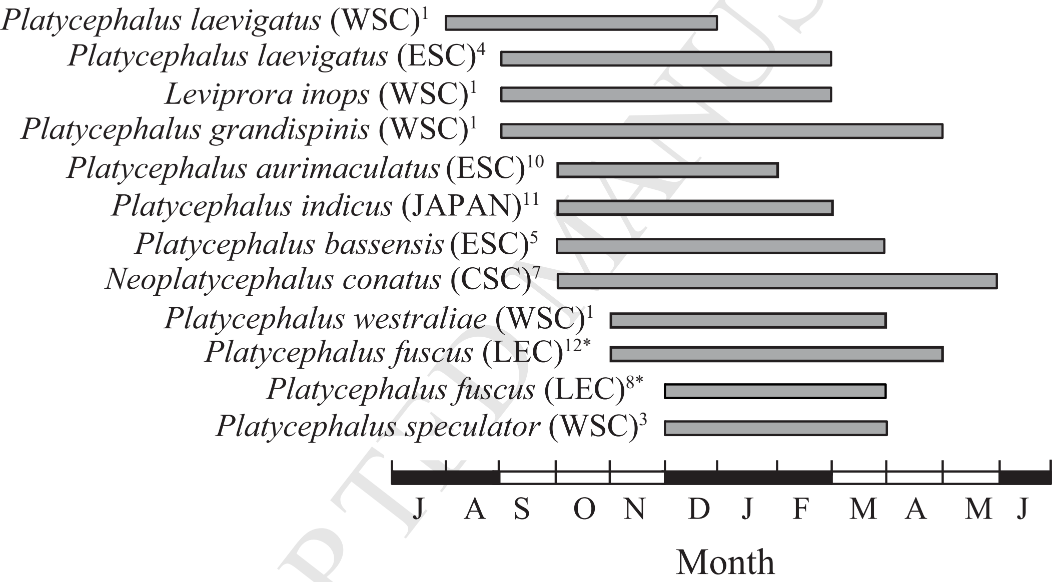
Supplementary Table 2. Mean and lower and upper 95% confidence limits for total lengths and ages for females (F) and males (M) of the five abundant platycephalid species in south-western Australia, derived from the upper deciles for those variables. * denotes length or age of sex of a species was significantly greater ($P < 0.05$) than that of the other sex of that species

		Total length (mm)			Age (years)		
Species	sex	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
P. westraliae	F	541*	529	553	6.3	6.0	6.7
P. westraliae	M	340	329	352	6.8	6.3	7.4
P. grandispinis	F	293*	286	300	7.6	7.0	8.2
P. grandispinis	M	234	225	244	9.1	7.8	10.1
P. speculator	F	486*	474	500	4.6	4.4	5.0
P. speculator	M	452	444	461	5.8*	5.3	6.3
P. laevigatus	F	519*	511	526	15.3	14.2	16.5
P. laevigatus	M	442	433	453	17.3	16.1	18.4
L. inops	F	600*	582	619	15.1	13.4	16.6
L. inops	M	471	458	486	13.8	12.7	15.0

Supplementary Table 3. Estimates of the TLs at which 50 and 95% of female and male *Platycephalus westraliae* and of female *Platycephalus grandispinis* (TL_{50} and TL_{95}, respectively) are mature and their upper and lower 95% confidence limits. No attempt was made to determine a maturity ogive for male *P. grandispinis* as virtually all males caught during the spawning period were mature.

		TL_{50} (mm)	**TL_{95} (mm)**	***a***
Platycephalus westraliae				
Female	**Estimate**	**269**	**336**	**0.04**
	Upper	288	354	0.05
	Lower	250	319	0.03
Male	**Estimate**	**185**	**252**	**0.04**
	Upper	212	283	0.05
	Lower	158	222	0.03
Platycephalus grandispinis				
Female	**Estimate**	**175**	**219**	**0.07**
	Upper	182	212	0.09
	Lower	169	225	0.05


a)
115˚E
125˚E
N
15˚S
25˚S
35˚S
Western Australia
SRE
WI
PRH
b)
Rottnest Island
Swan River Estuary
Comet Bay
5 km
c)
Wilson Inlet
2.5 km
d)
Oyster Harbour
Princess Royal Harbour
King George Sound
5 km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Platycephalus laevigatus (ESC)[4]
Leviprora inops (WSC)[1]
Platycephalus grandispinis (WSC)[1]
Platycephalus aurimaculatus (ESC)[10]
Platycephalus indicus (JAPAN)[11]
Platycephalus bassensis (ESC)[5]
Neoplatycephalus conatus (CSC)[7]
Platycephalus westraliae (WSC)[1]
Platycephalus fuscus (LEC)[12*]
Platycephalus fuscus (LEC)[8*]
Platycephalus speculator (WSC)[3]
J
A
S
O
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M
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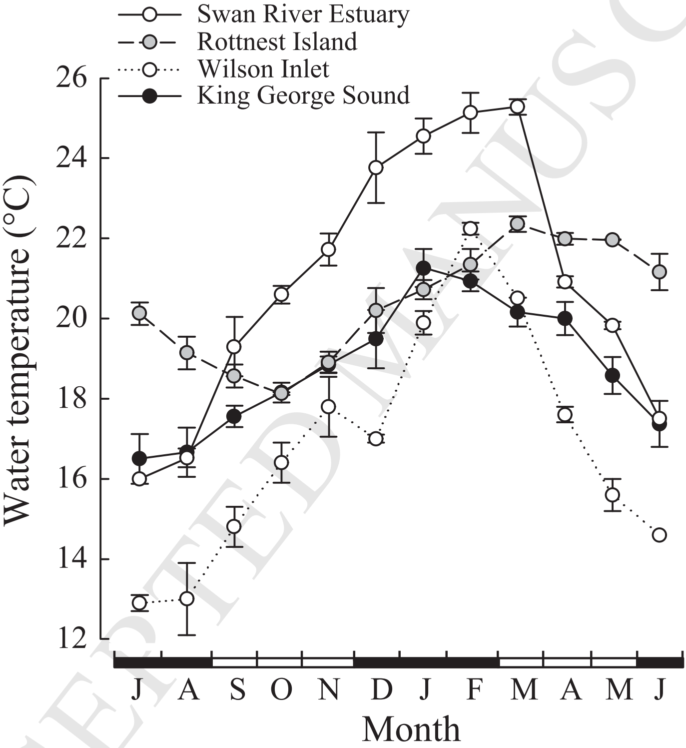
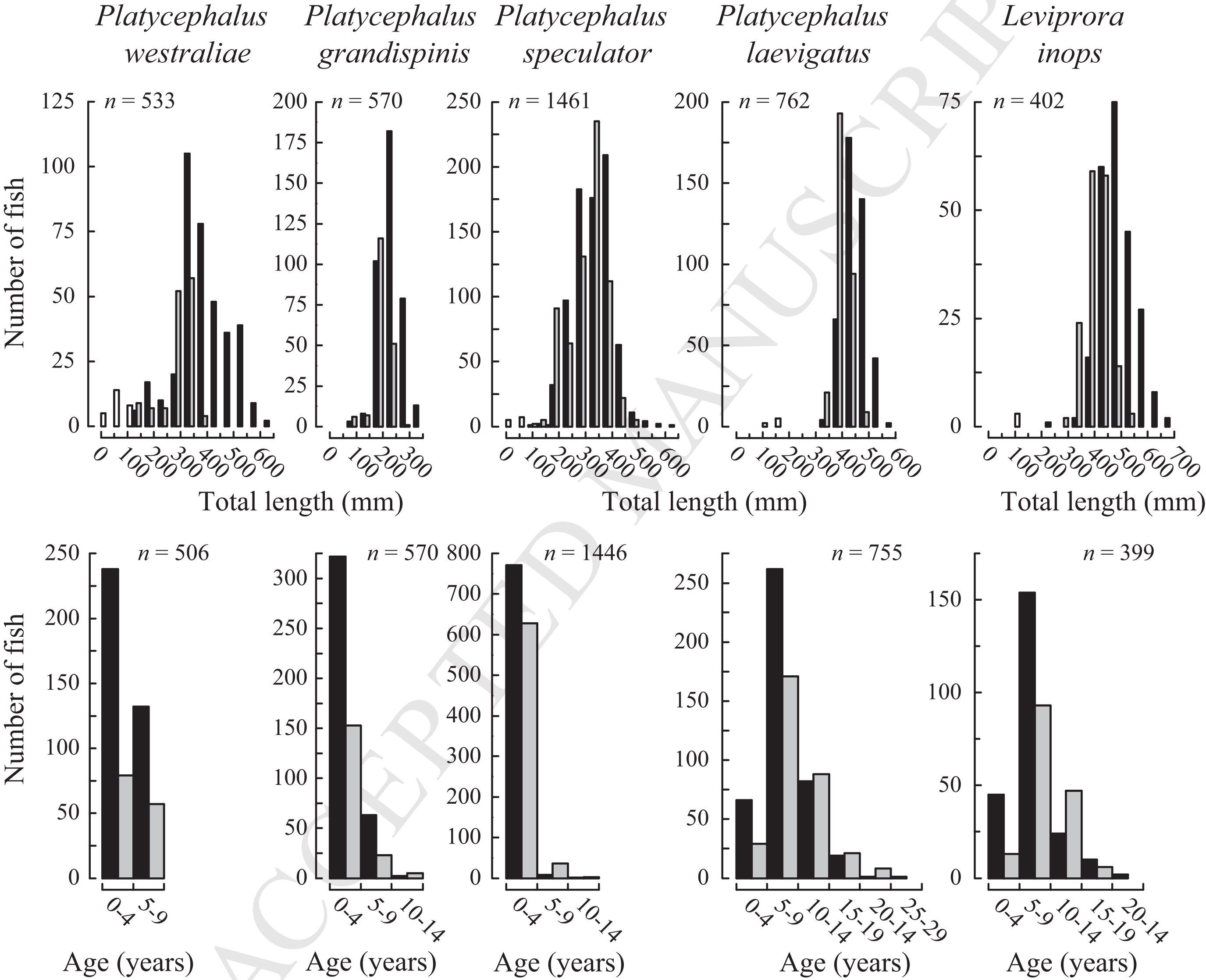
Month


Swan River Estuary
Rottnest Island
Wilson Inlet
King George Sound
Water temperature (°C)
26
24
22
20
18
16
14
12
J
A
S
O
N
D
J
F
M
A
M
J
Month



Platycephalus westraliae
Platycephalus grandispinis
Platycephalus speculator
Platycephalus laevigatus
Leviprora inops
Number of fish
n = 533
n = 570
n = 1461
n = 762
n = 402
125
100
75
50
25
0
200
175
150
125
100
75
50
25
0
250
200
150
100
50
0
200
150
100
50
0
75
50
25
0
0 100 200 300 400 500 600
0 100 200 300
0 100 200 300 400 500 600
0 100 200 300 400 500 600
0 100 200 300 400 500 600 700
Total length (mm)
Total length (mm)
Total length (mm)
Number of fish
n = 506
n = 570
n = 1446
n = 755
n = 399
250
200
150
100
50
0
300
250
200
150
100
50
0
800
700
600
500
400
300
200
100
0
250
200
150
100
50
0
150
100
50
0
0-4 5-9
0-4 5-9 10-14
0-4 5-9 10-14
0-4 5-9 10-14 15-19 20-14 25-29
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Age (years)
Age (years)
Age (years)
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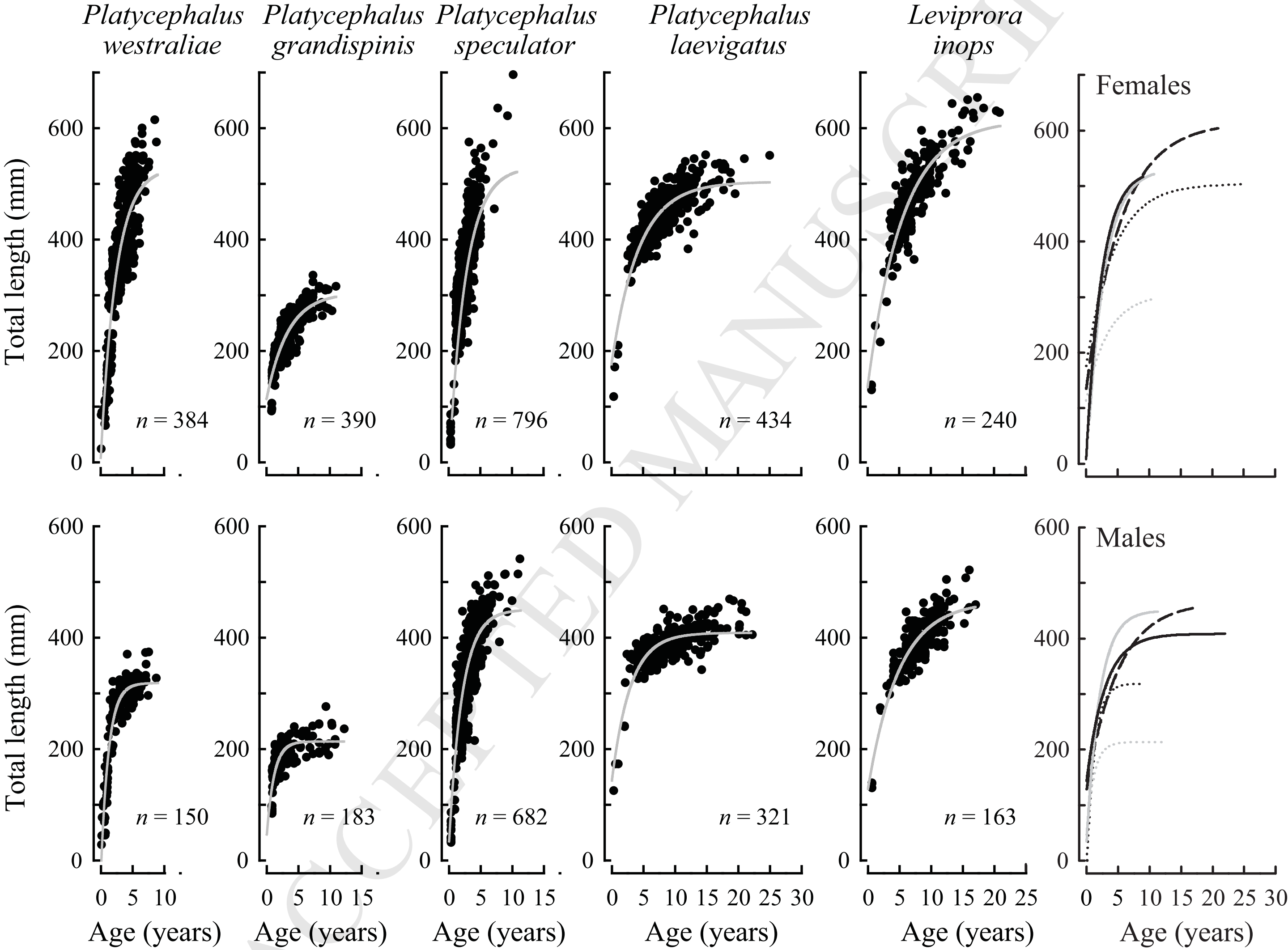
Age (years)


Platycephalus westraliae
Platycephalus grandispinis
Platycephalus speculator
Platycephalus laevigatus
Leviprora inops
Females
Males
Total length (mm)
Total length (mm)
0
200
400
600
n = 384
n = 390
n = 796
n = 434
n = 240
n = 150
n = 183
n = 682
n = 321
n = 163
0
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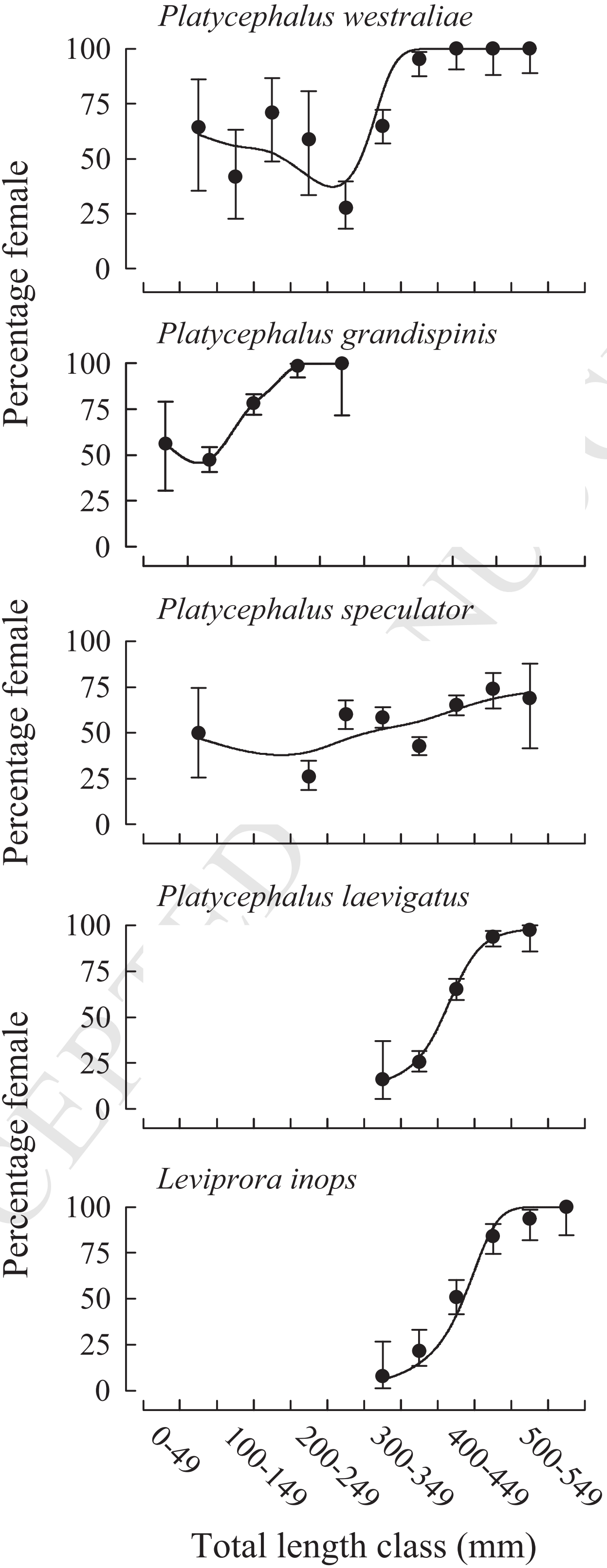
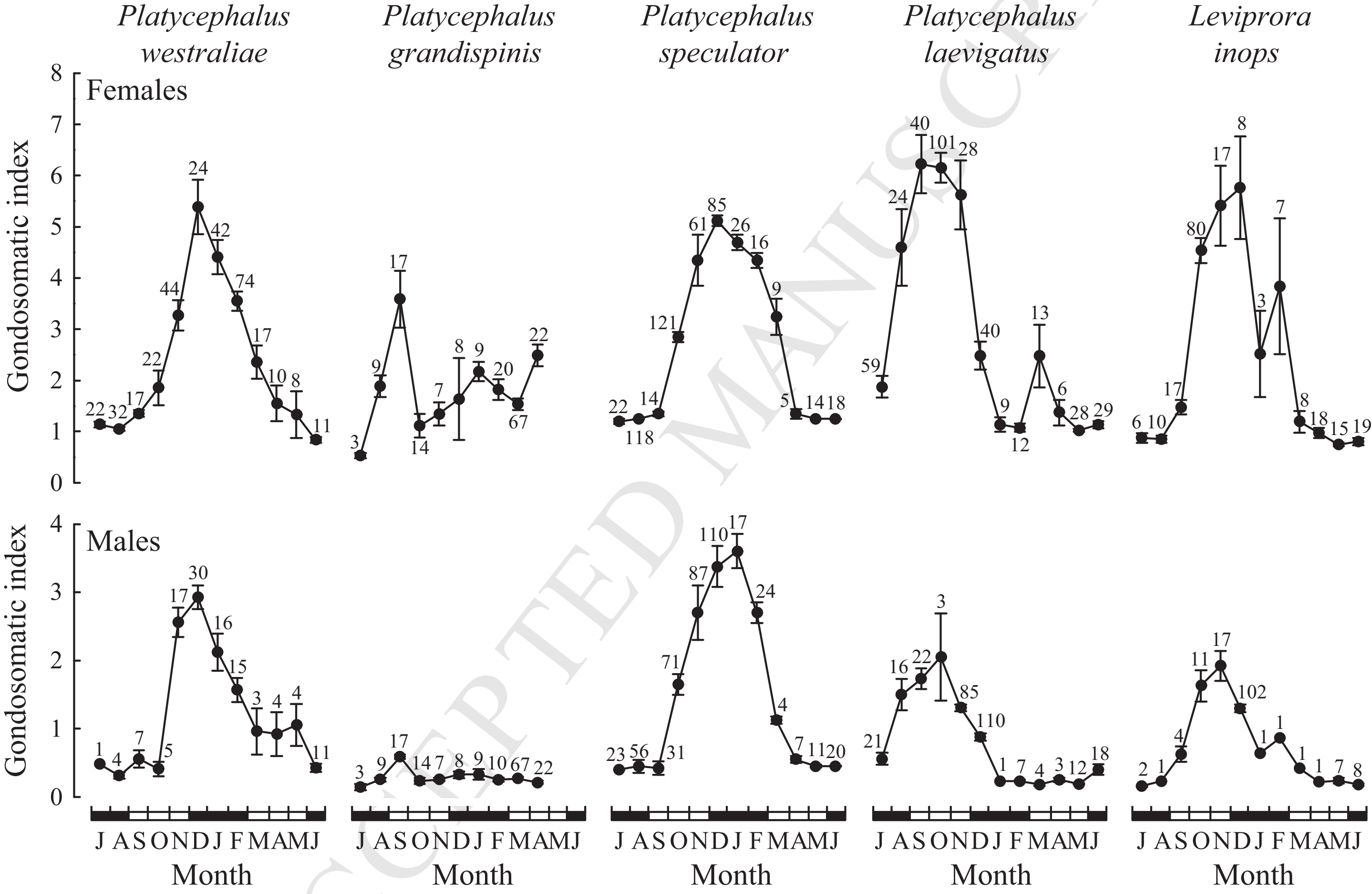
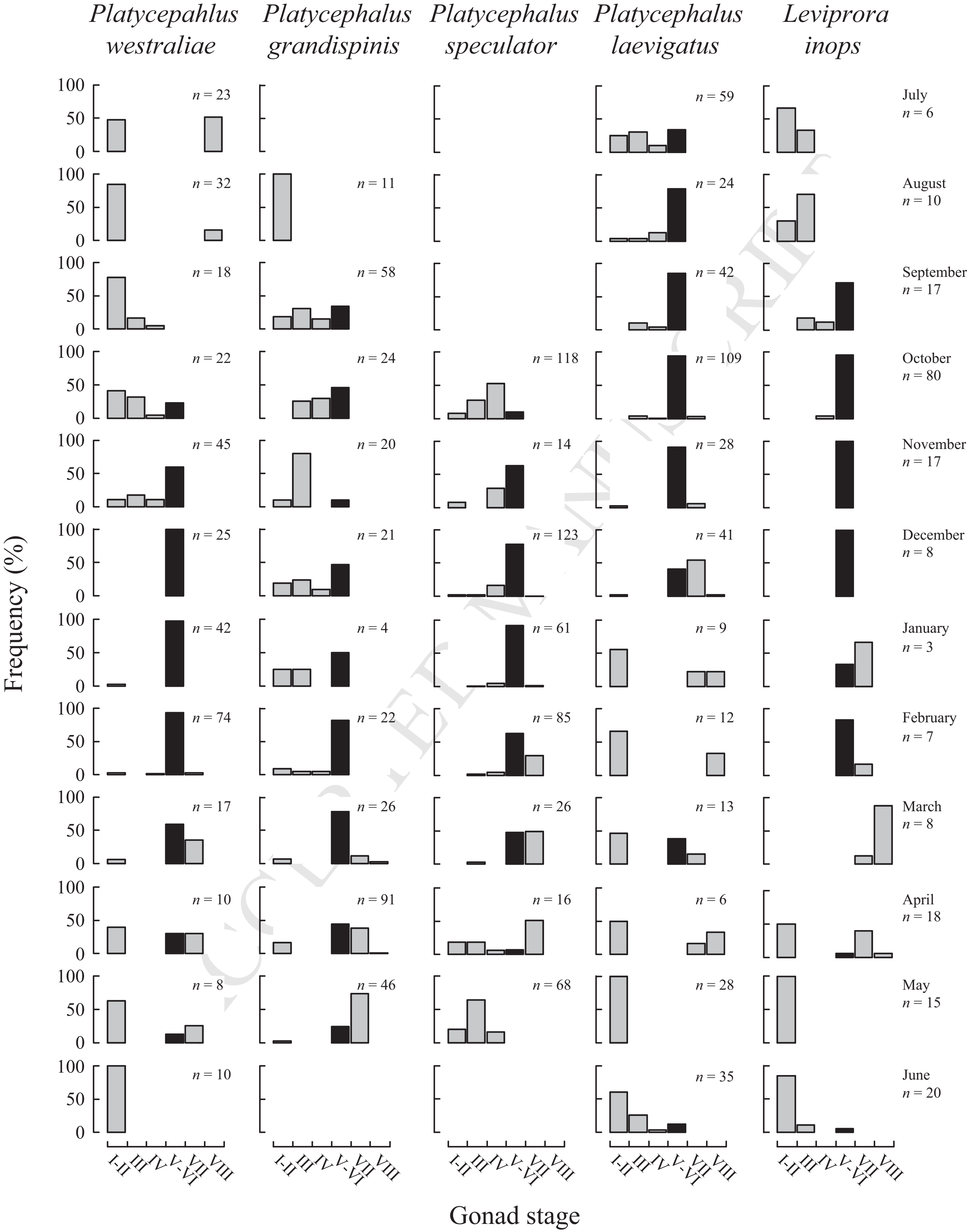
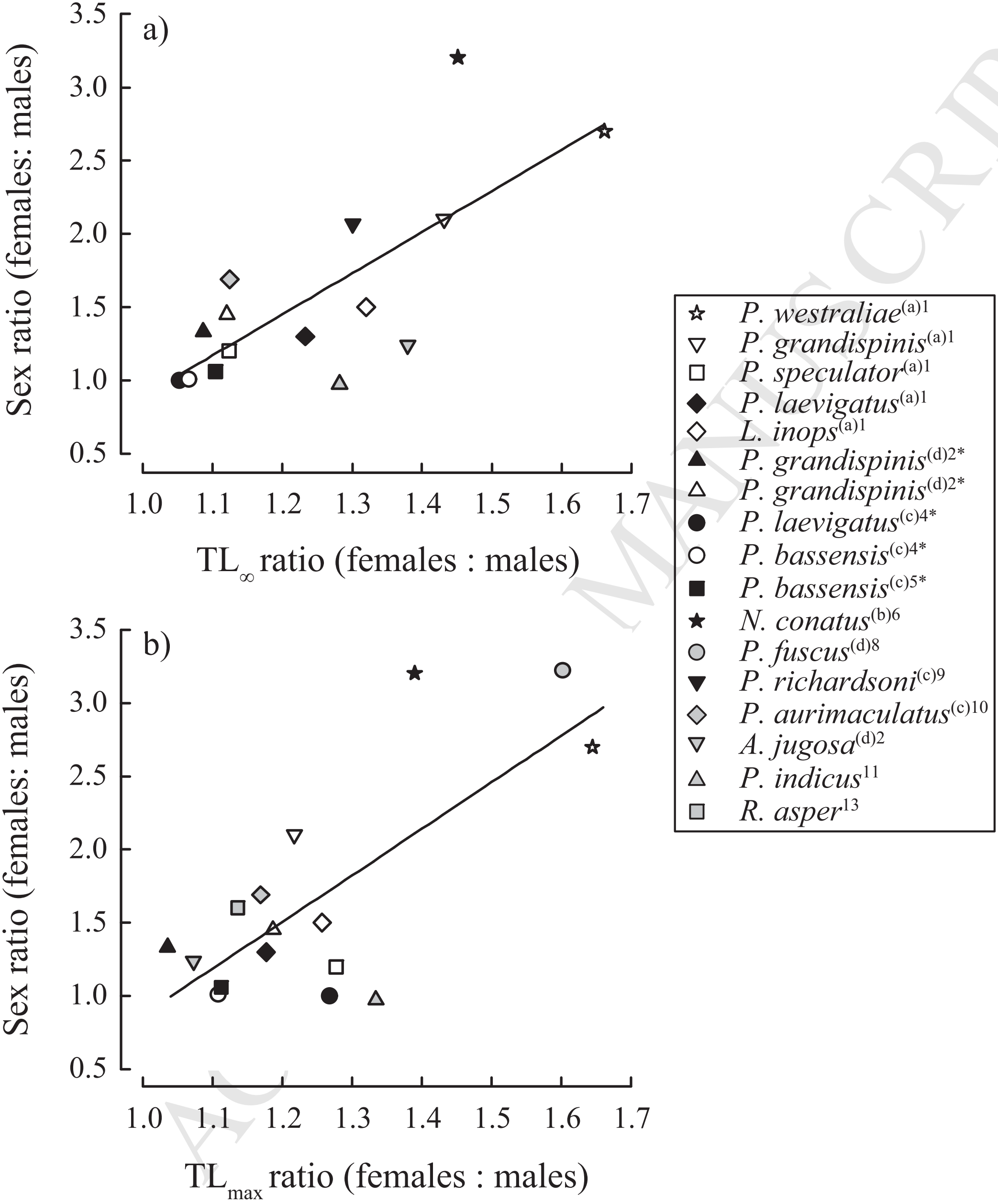
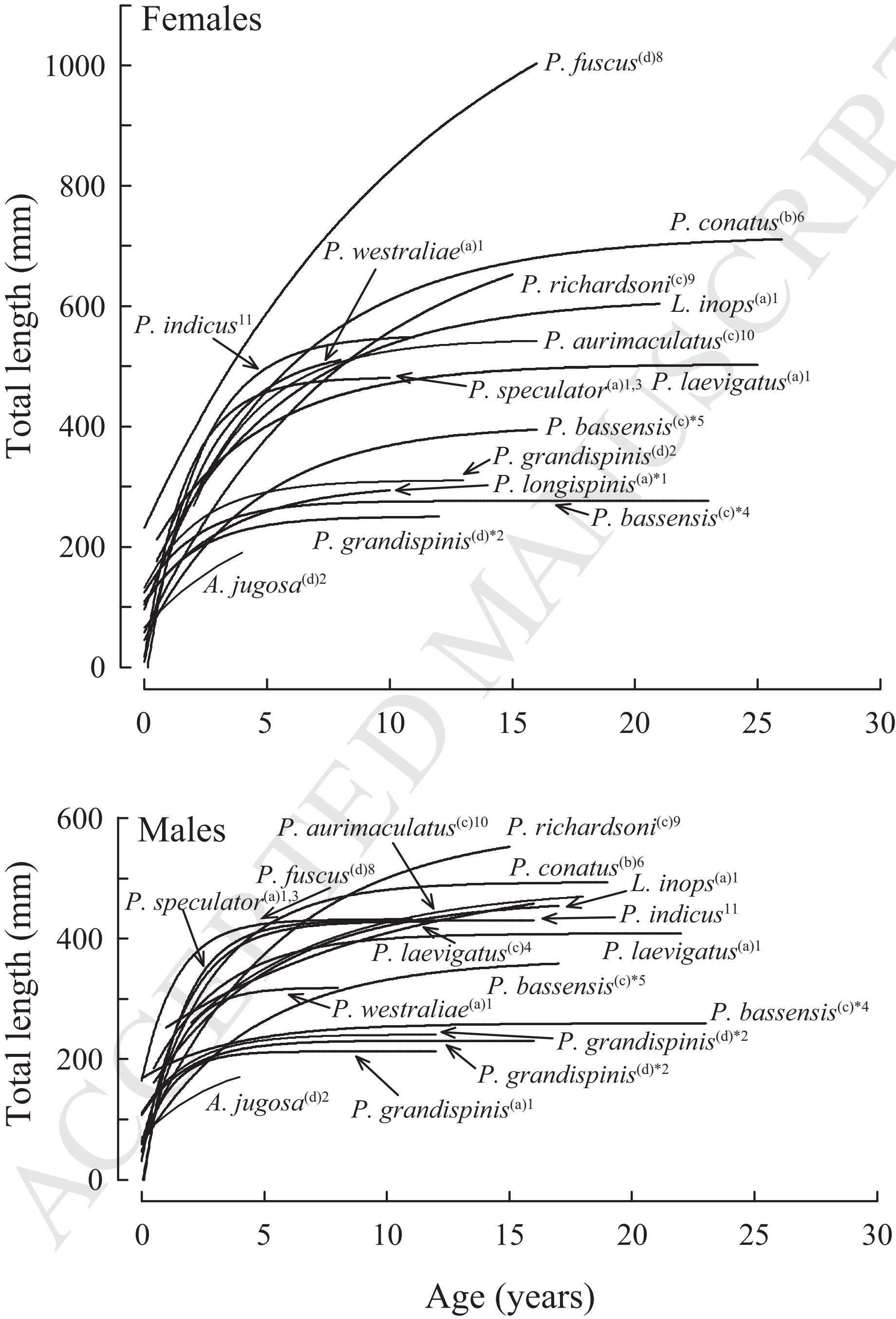
10
15
20
25
30
Age (years)
Age (years)
Age (years)
Age (years)
Age (years)
Age (years)


Platycephalus westraliae
Platycephalus grandispinis
Platycephalus speculator
Platycephalus laevigatus
Leviprora inops
Percentage female
Percentage female
Percentage female
Percentage female
100
75
50
25
0
0-49
100-149
200-249
300-349
400-449
500-549
Total length class (mm)


Platycephalus westraliae
Platycephalus grandispinis
Platycephalus speculator
Platycephalus laevigatus
Leviprora inops
Females
Males
Gondosomatic index
Gondosomatic index
0
1
2
3
4
5
6
7
8
0
1
2
3
4
22 32 17 22 44 24 42 74 17 10 8 11
3 9 17 14 7 8 9 20 67 22
22 118 14 121 61 85 26 16 9 5 14 18
59 24 40 101 28 40 9 12 13 6 28 29
6 10 17 80 17 8 3 7 8 18 15 19
1 4 7 5 17 30 16 15 3 4 4 11
3 9 17 14 7 8 9 10 67 22
23 56 31 71 87 110 17 24 4 7 11 20
21 16 22 3 85 110 1 7 4 3 12 18
2 1 4 11 17 102 1 1 1 1 7 8
J A S O N D J F M A M J
Month


Platycepahlus westraliae
Platycephalus grandispinis
Platycephalus speculator
Platycephalus laevigatus
Leviprora inops
100
50
0
July n = 6
August n = 10
September n = 17
October n = 80
November n = 17
December n = 8
January n = 3
February n = 7
March n = 8
April n = 18
May n = 15
June n = 20
n = 23
n = 59
n = 32
n = 11
n = 24
n = 18
n = 58
n = 42
n = 22
n = 24
n = 118
n = 109
n = 45
n = 20
n = 14
n = 28
n = 25
n = 21
n = 123
n = 41
n = 42
n = 4
n = 61
n = 9
n = 74
n = 22
n = 85
n = 12
n = 17
n = 26
n = 26
n = 13
n = 10
n = 91
n = 16
n = 6
n = 8
n = 46
n = 68
n = 28
n = 10
n = 35
Frequency (%)
I-II
III
IV
V-VI
VII
VIII
Gonad stage


a)
Sex ratio (females: males)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
TL$_\infty$ ratio (females : males)
b)
Sex ratio (females: males)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
TL$_{max}$ ratio (females : males)
☆ *P. westraliae*$^{(a)1}$
▽ *P. grandispinis*$^{(a)1}$
□ *P. speculator*$^{(a)1}$
◆ *P. laevigatus*$^{(a)1}$
◇ *L. inops*$^{(a)1}$
▲ *P. grandispinis*$^{(d)2*}$
△ *P. grandispinis*$^{(d)2*}$
● *P. laevigatus*$^{(c)4*}$
○ *P. bassensis*$^{(c)4*}$
■ *P. bassensis*$^{(c)5*}$
★ *N. conatus*$^{(b)6}$
● *P. fuscus*$^{(d)8}$
▼ *P. richardsoni*$^{(c)9}$
◆ *P. aurimaculatus*$^{(c)10}$
▽ *A. jugosa*$^{(d)2}$
▲ *P. indicus*^{11}
■ *R. asper*^{13}


Females
Total length (mm)
0
200
400
600
800
1000
P. fuscus(d)8
P. conatus(b)6
P. westraliae(a)1
P. richardsoni(c)9
L. inops(a)1
P. indicus11
P. aurimaculatus(c)10
P. speculator(a)1,3
P. laevigatus(a)1
P. bassensis(c)*5
P. grandispinis(d)2
P. longispinis(a)*1
P. bassensis(c)*4
P. grandispinis(d)*2
A. jugosa(d)2
0
5
10
15
20
25
30
Males
Total length (mm)
0
200
400
600
P. aurimaculatus(c)10
P. richardsoni(c)9
P. conatus(b)6
P. fuscus(d)8
L. inops(a)1
P. speculator(a)1,3
P. indicus11
P. laevigatus(c)4
P. laevigatus(a)1
P. bassensis(c)*5
P. westraliae(a)1
P. bassensis(c)*4
P. grandispinis(d)*2
P. grandispinis(d)*2
A. jugosa(d)2
P. grandispinis(a)1
0
5
10
15
20
25
30
Age (years)

Highlights

- Female platycephalids grow larger than males, but longevities of sexes are similar.
- Proportion of females is related to extent that females are larger than males.
- Growth, size and numbers of females of estuarine species far exceed those of males.
- Growth is main factor contributing to marked differences in sex ratios.
- Spawning periods of species overlap, but occur latest in estuarine residents.