



Biological characteristics of the non-indigenous *Acentrogobius pflaumii* (Bleeker 1853) in a warm-temperate estuary, and thus very different from its typical environment

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ABSTRACT

The gobiid *Acentrogobius pflaumii*, native to estuaries and coastal embayments in East Asia, has recently established a population in the warm-temperate Swan-Canning Estuary (SCE) in southwestern Australia. Data from 432 individuals demonstrated that although *A. pflaumii* was shown to live for ~4 years, the age composition was dominated by 0+ and 1+ individuals. The maximum size of female (94 mm) and male (96 mm) *A. pflaumii* in the SCE is 33% larger than in its native habitat. *Acentrogobius pflaumii* grew rapidly, attaining a length of ~65 mm, i.e. 84 and 87% of their TL_{∞} 's of 77.3 and 72.9 mm for females and males, respectively, within the first year of life. Gonadosomatic indices, trends in monthly gonadal development and histological examination of gonads indicate that, although peak spawning in the SCE occurs over a similar period and season as in South Korean waters, spawning is more protracted in the SCE. Two discrete modes in oocyte diameter frequencies indicate this species exhibits determinate fecundity. The protracted spawning period enables batches of eggs to be released periodically during favourable conditions. These biological traits are likely to have aided in the successful colonisation of this species in the SCE. Quantifying the phenotypic plasticity of this non-indigenous species may inform risk assessments and subsequent management plans to mitigate the effect of *A. pflaumii* in the SCE and predict the likelihood of it colonising other southwestern Australian estuaries.

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1. Introduction

Non-indigenous fish species have the potential to outcompete and displace native species (e.g. Pelicice et al., 2015; Hempel et al., 2018; Júza et al., 2018), thus posing a threat to native fish communities. Many introduced species possess life history characteristics, such as fast growth and high fecundity and very plastic life-histories, which enable them to proliferate rapidly in different environments (Davidson et al., 2011; Beatty et al., 2017; Kornis et al., 2017). Due to their small size, crevicolous nature and habit of creating burrows, gobiids avoid detection and escape predation and are amongst the world's most invasive fish species (Carlton et al., 1995; Wonham et al., 2000). The dispersal and establishment of gobiids and other species outside their typical range has been facilitated by increases in shipping activity, particularly after the 1960s when ships took on greater volumes of ballast water (Carlton, 1996). The discharge of ballast water in ports, many of which are located near the mouths of estuaries,

has led to these productive environments becoming hotspots for invasion for a host of aquatic species, particularly fishes (e.g. Ruiz et al., 1997; Thresher, 1999; Hewitt et al., 2004).

Members of the Gobiidae exhibit variable longevity, with ages ranging from as young as 59 days for *Eviotta silligata*, to as old as 13 years for *Gobiodon okinawae* (Depczynski and Bellwood, 2005; Randall and Delbeek, 2009). Such varied longevity has led to gobiids being aged using daily growth zones in otoliths for shorter lived species (e.g. Iglesias et al., 1997; Hernaman et al., 2000; Iida et al., 2010; Winterbottom et al., 2011) and annual growth zones in otoliths for longer lived species (e.g. Kovačić, 2006; Gumus and Kurt, 2009; Kornis et al., 2017). Gobiid species, with typically short lifecycles, often display rapid growth, and, in comparison to larger fishes, experience relatively little, if any time at asymptotic size before death (e.g. Gill et al., 1996; Depczynski and Bellwood, 2005; Hernaman and Munday, 2005). Shorter lifespans, with accelerated growth, are considered a characteristic of most gobiids, and particularly smaller species, e.g. those in the genus *Eviota*, which display rapid linear growth throughout the entirety of their short (<100 days) lives (Depczynski and Bellwood, 2006). Other species, such as *Pseudogobius olorum*, which lives for ~12

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months, exhibit very rapid growth, with von Bertalanffy growth coefficients (k) of $>7 \text{ year}^{-1}$ (Gill et al., 1996). Larger, longer-lived gobies tend to have breeding seasons with multiple spawning-events, typically during the spring and summer months, while smaller, shorter-lived gobiids have generally more protracted or biannual spawning seasons (e.g. Gill et al., 1996; La Mesa, 2001; Mazzoldi and Rasotto, 2001; La Mesa et al., 2005). Gobies are a very speciose family with 189 genera and 1359 species that display a range of life-history strategies, (Fricke et al., 2019), typically they attain sexual maturity at a relatively early age, which is likely an adaptation to predation pressure (e.g. Hernaman and Munday, 2005; Depczynski and Bellwood, 2006).

Together with atherinids, gobiids dominate the fish faunas of the nearshore waters of microtidal estuaries, such as those in southwestern Australia (Loneragan et al., 1986, 1989; Potter et al., 2016; Tweedley et al., 2016; Valesini et al., 2017). Despite their abundance, there is a paucity of data on the biological characteristics of gobiid species in southwestern Australia and the Swan-Canning Estuary (SCE). These limited studies demonstrate, however, that *Arenigobius bifrenatus* and *P. olorum*, both of which complete their lifecycle within estuaries (Potter et al., 2015a) and typically reside in the upper reaches of these systems (Gill and Potter, 1993), spawn during spring and summer (Gill et al., 1996). While the exact spawning duration of *A. bifrenatus* is unknown, *P. olorum* exhibits more biannual spawning, with multiple recruitment phases throughout its short, <12 month, lifespan (Gill et al., 1996).

The Striped Sandgoby, *Acentrogobius pflaumii*, is native to estuaries and coastal embayments in China, Korea, Japan, Taiwan and the Philippines, inhabiting sand and seagrass substrates (Masuda et al., 1984; Shao et al., 1993; Horinouchi and Sano, 2000; Kanou et al., 2004; Horinouchi, 2008; Nan et al., 2009). Following translocation, likely via ballast water discharge, *A. pflaumii* has established populations in Waitemata and Whanapoua harbours, New Zealand, and Moreton Bay and Port Phillip Bay in eastern Australia (Lockett and Gomon, 2001; Gomon et al., 2008). The species was first recorded in Western Australia in Cockburn Sound, a marine embayment in the lower-west coast in 2004 (Mead-Hunter, 2005) and later recorded in the SCE, ~ 20 km to the north (Maddern and Morrison, 2009).

The establishment of *A. pflaumii*, a species with relatively little available life history information, in the SCE provided the unique opportunity to investigate the biological attributes of a species outside its typical distribution and how those attributes have allowed it to establish populations in non-native environments. This information has the potential to inform management plans for restricting the proliferation of non-indigenous species (Kornis et al., 2017). Thus, the aims of this study were to: (1) establish appropriate ageing protocols for *A. pflaumii* using increments in their otoliths and to validate the periodicity of the formation of such increments; (2) determine the growth rates for female and male *A. pflaumii*; and (3) determine whether *A. pflaumii* spawns in the SCE and, if so, the timing and duration of spawning and the length and ages at maturity for females and males. As the SCE possesses warmer water temperatures throughout the year than in *A. pflaumii*'s natal distribution in Korea, it is hypothesised that the population will exhibit more rapid growth and attain a larger size in the SCE than natal environments and that the spawning period of this species will be more protracted than in its native environments.

2. Materials and methods

2.1. Sampling methodology

A total of 432 *A. pflaumii* were collected following monthly otter trawling at 16 sites in offshore (2–17 m deep) waters of

the SCE at $\sim 32^\circ\text{S}$ in southwestern Australia between July 2014 and September 2015 (see Broadley et al., 2017; Poh et al., 2019 for full sampling details). The otter trawl net (4.4 m headline length, 2.6 m wing-end spread), with 25 mm mesh in the body, and 9 mm mesh in the cod end was towed at a speed of ~ 1.6 knots ($\sim 3 \text{ km h}^{-1}$) for 5 min in deeper, offshore waters of the estuary. A rigorous sampling programme was also carried out in the shallow water <1.5 m at the same time using hand-trawl nets (4 m wide, constructed from 9 mm mesh), but no *A. pflaumii* were caught on any of the 1240 occasions that hand trawls were used. This sampling programme was designed to catch Western School Prawns *Metapenaeus dalli*, a species that buries in the substratum, along the length of the SCE up to 35 km from the estuary mouth. Although the size of mesh of the trawl net, particularly the wings, was quite large in comparison to the size of *A. pflaumii*, this net did catch other small benthic fish and prawns (i.e. <40 mm in total length), and thus the samples of *A. pflaumii* collected by this net are thought to accurately represent the population present in the estuary. The total length (TL) and total weight (TW) of each *A. pflaumii* was measured to the nearest 1 mm and 0.1 g, respectively, and sagittal otoliths were removed, cleaned and dried, before being stored in gelatine capsules within labelled seed envelopes. Water temperature at the bottom of the water column at each sampling site, on each sampling occasion was recorded to the nearest 0.1°C using a YSI 556 MPS handheld multiparameter instrument.

2.2. Age determination and validation

Whole otoliths were placed, proximal surface up, in a small, black glass dish, covered in immersion oil (type B), and photographed under reflected light using a Leica DFC425 digital camera attached to a Leica MZ75 dissecting microscope (Fig. 1). The numbers of opaque zones, clearly delineated from the primordium, in each otolith were identified by K. Hogan-West and marked using Leica Application Suite (LAS v.3.6). All otoliths were also independently read by a second independent and experienced otolith reader (P.G. Coulson) and the level of precision between the counts of the two readers assessed using the coefficient of variation (Chang, 1982). The resultant CV of 3.3%, is well below the 5% considered acceptable by Campana (2001), demonstrating that there was a high level of agreement between the counts of the two readers.

Marginal increment analysis was used to identify the periodicity of the formation of the opaque bands in the otoliths of *A. pflaumii*. Marginal increment analysis, 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 two or more such zones were present. All measurements were taken along the same axis (i.e. horizontally, towards the ventral edge, in alignment with the primordium) on the same digital images employed when counting the number of opaque zones. Further confirmation of the annual formation of opaque zones in the otoliths of *A. pflaumii* was carried out by statistically demonstrating the trends exhibited by the monthly marginal increments throughout the year conform to a single cycle (Coulson et al., 2016, 2017). 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 30th 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.

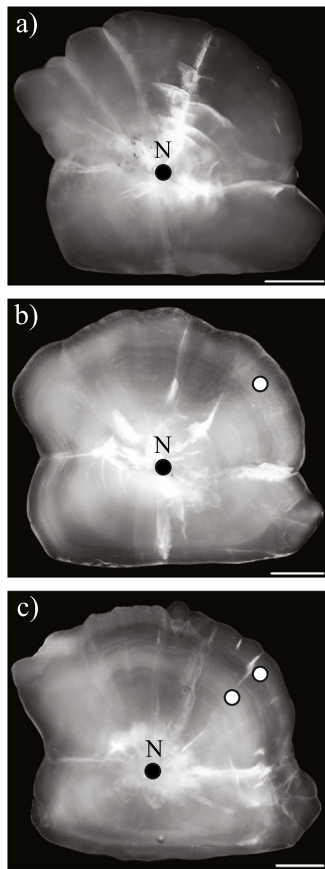


Fig. 1. *Acentrogobius pflaumii* otoliths with (a) zero, (b) one and (c) two opaque zones. Black dot in all images denotes the position of the nucleus (N), white dots in (b) and (c) denote delineated opaque zones. Scale = 0.5 mm.

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).

2.3. Growth determination

The age of each *A. pflaumii* was estimated using the date of capture, an average “birthdate” of 1st December (approximate mid-point of spawning period; see later), the number of opaque zones in its otolith and the timing of formation of those zones. The von Bertalanffy growth curves were fitted separately to the lengths at ages of female and male *A. pflaumii* in R (v. 3.1.1.) using a non-linear ‘growth’ function in the package ‘Fish methods’ (Nelson, 2015). Individuals that could not be sexed were excluded from the dataset. The von Bertalanffy growth equation is $TL = TL_{\infty} (1 - \exp(-k(t - t_0)))$ where TL is the total length (mm) at age t (years), TL_{∞} is the mean asymptotic total length, k is the growth coefficient (year^{-1}) and t_0 is the theoretical age (years) at which the fish would have zero length. Due to the lack of small individuals (i.e. <40 mm), the values for t_0 for females and males were highly negative and, biologically, not realistic and as a result t_0 was determined as follows: *A. pflaumii* are known to settle at a length of 5–8 mm after a pelagic larval phase of 30 days (Lockett and Gomon, 2001; Kanou et al., 2004), thus von Bertalanffy growth curves were fitted to the lengths at age of females and males with t_0 constrained to 0.08 years (~30 d) for both sexes. A likelihood-ratio test (Cerrato, 1990) was used to compare the growth of female and male *A. pflaumii*.

2.4. Reproductive biology

The ovaries and testes of female and male *A. pflaumii*, respectively, were removed and weighed to the nearest 0.0001 g wet weight. Gonads of all individuals were examined using a dissecting microscope, sexed and allocated to one of seven stages of development, modified from Laevastu's (1965) criteria, which were condensed into the four following groupings: II = immature virgin/resting adult; III/IV = developing/maturing; V/VI = mature/spawning; VII/VIII = spent/recovering. A subsample of gonads at each macroscopically identified developmental stage, in each month, was placed in Bouin's solution for a minimum of 24 h, dehydrated in an ascending series of ethanol concentrations and embedded in paraffin wax. Transverse sections of the mid-region of each gonad were taken, stained with Mallory's trichrome, mounted on glass microscope slides and then used to confirm the allocation of gonads to the appropriate macroscopic stages.

The frequencies of gonads at each stage of development in each month were used to help identify the timing and duration of spawning for *A. pflaumii* in the SCE. The gonadosomatic index (GSI) for females and males, which has routinely been used for a number of fish species in the SCE (Prince and Potter, 1983; Gill et al., 1996; Sarre and Potter, 1999), was calculated using the following equation, $GSI = (GW/TW) \times 100$, where GW = wet gonad weight and TW = total wet body weight. The resultant values were then plotted as pooled monthly means for each sex to demonstrate the annual reproductive cycle. As the majority of female and male *A. pflaumii* caught during the spawning period (see later), which were 45–94 mm and 46–96 mm, respectively, possessed mature gonads (i.e. stages III–VIII), all fish collected during this study were used to determine the timing and duration of spawning.

To ascertain whether *A. pflaumii* have determinate or indeterminate fecundity *sensu* (Hunter and Macewicz, 1985), the distribution of the diameters of ~ 50 randomly-selected oocytes in histological sections of stage V ovaries of five females, collected in October, were measured. The diameter of oocytes in digital images of the histological sections of ovaries, taken using the same microscope and camera used for imaging otoliths, were derived from measurements made of the circumference of that oocyte to the nearest 0.01 μm using LAS (v.3.6). Note that measurements were restricted to oocytes in which the nucleus was clearly visible to ensure that the oocyte had been sectioned through its centre. The stage in the development of each measured oocyte was recorded, i.e. early previtellogenic, cortical alveolar or yolk granule oocyte.

3. Results

3.1. Marginal increment analysis

Mean monthly marginal increments (MI) for whole otoliths of *A. pflaumii* with one opaque zone increased from low values in February (late summer) to a maximum (0.2) in June (early winter), after which the mean monthly MI decreased rapidly to low levels (~0.1) in September to November (early to late spring; Fig. 2a). Overall, a similar trend was exhibited for *A. pflaumii* with 2–3 opaque zones, with the mean marginal increment reaching a maximum in June (~0.4), after which it declined (~0.2; Fig. 2b).

The presence of a single pronounced rise and decline throughout the year displayed by fish with 2–3 growth zones, and, to lesser extent, fish with one opaque zone, represents the pronounced sinusoidal cycle required to substantiate the formation of a single opaque zone per year. For otoliths with a single opaque zone, this conclusion is substantiated by the results of circular

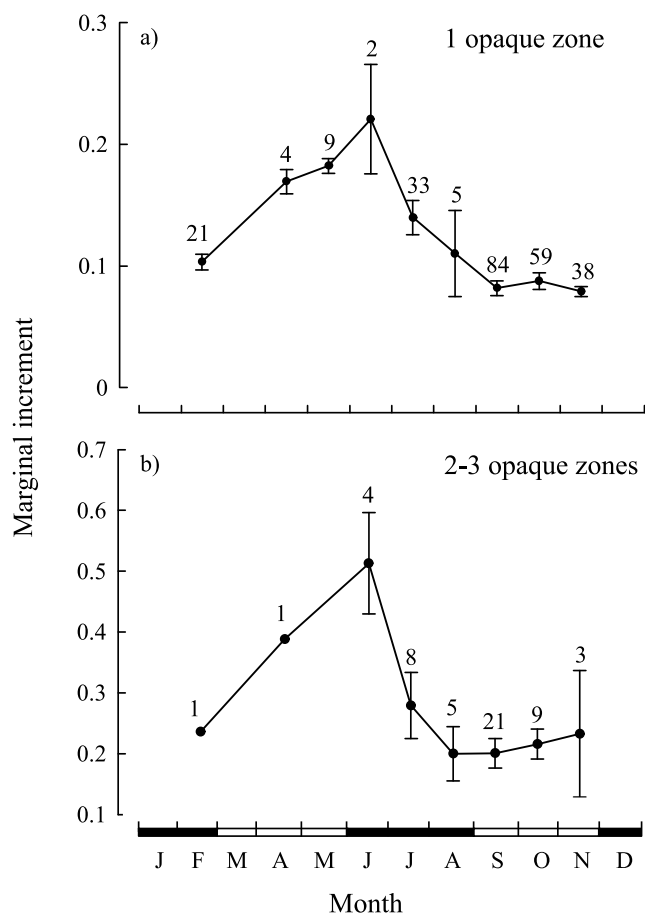


Fig. 2. Mean monthly marginal increments (± 1 SE) for *Acentrogobius pflaumii* whole otoliths with (a) one and (b) two to three opaque zones. On the x-axis closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months.

distribution models (Okamura and Semba, 2009) and concomitant AIC values. Thus, the AIC was less for an annual cycle (296) than no cycle (312) or a biannual cycle (305). Furthermore, the difference between the lowest AIC and the other AIC for each group of otoliths was >2 , the number required to identify definitively the best model in terms of the Kullback–Leibler distance (Burnham and Anderson, 2002). The smaller numbers of otoliths with 2–3 opaques zones between January and May prohibited the fitting of the circular distribution models. A combination of the pattern in the mean monthly marginal increments and the circular distribution models (for otoliths with one opaque zone), demonstrate that the number of opaque zones in *A. pflaumii* otoliths can be used to calculate its age.

3.2. Length and age frequencies

The 277 female and 127 male *A. pflaumii* collected from the SCE (SCE) ranged in length from 45–94 mm and 46–96 mm, respectively (Fig. 3a). The sex of 14 fish (45–60 mm) could not be determined. Females were substantially more abundant than males, both overall, and in each length class up to 80 mm, above which males were more abundant (Fig. 3b). Females were most abundant in the 61–65 and 66–70 mm length classes, while males, although exhibiting relatively uniform frequencies in those length classes between 56 and 75 mm, were most abundant in the 66–70 mm length class.

Samples of both sexes of *A. pflaumii* were dominated by individuals in the 1+ age class. Female *A. pflaumii* dominated both

Table 1

von Bertalanffy growth parameters for asymptotic total length (TL_{∞}) and growth coefficient (k) for individual length at age data for *Acentrogobius pflaumii* in the Swan-Canning Estuary. Note, the estimated age at zero length, t_0 , has been fixed at 0.08 years, representing an age of 30 days, which is the duration of pelagic phase of *A. pflaumii*, after which fish settle at a length of 5–8 mm (Lockett and Gomon, 2001; Kanou et al., 2004).

Sex		TL_{∞}	k	t_0	r^2	n
Females	Estimate	69.3	2.74	0.08	0.16	277
	Upper	70.8	3.21			
	Lower	67.9	2.38			
Males	Estimate	74.9	2.06	0.08	0.23	128
	Upper	77.7	2.55			
	Lower	72.6	1.69			

the 0+ and 1+ age classes with 92 and 147 individuals, respectively, compared to 32 (74.1% females) and 60 individuals (71.0% females), respectively, for males (Fig. 3b). In the 0+ and 1+ age classes, the ratios of females to males of 2.8:1 and 2.4:1, respectively, differed significantly from parity (both $P < 0.001$, $\chi^2 = 29.0$ and $\chi^2 = 36.6$, respectively). The ratio of females and males in the 2+ age class (1.2:1) was close to parity ($P = 0.5$, $\chi^2 = 0.5$), while of the six fish in 3+ age class, only one was female (Fig. 2). The overall sex ratio of 2.2 females to 1.0 male differs significantly from parity ($P < 0.001$, $\chi^2 = 55.1$).

3.3. Growth

The von Bertalanffy growth curves with t_0 fixed to 0.08 years, for females and males, visually, provided a good fit to the lengths at age for each sex, despite considerable variation in length at age for both sexes, as reflected by the low r^2 values (0.16 for females and 0.23 for males, Fig. 4; Table 1). The likelihood ratio test demonstrated that the growth of female and male *A. pflaumii* differed significantly ($P < 0.05$). Thus, based on the curves, the TL for females and males at 1 year of age were both, on average, 65 mm, while at 2 years of age females were 69 mm and males were 74 mm. The growth coefficient (k) values for each sex, indicate that both sexes exhibit rapid growth early in life to attain a length close to their TL_{∞} by the end of their first year of life (Fig. 4). The higher k value for females (2.74 y^{-1}) than males (2.06 y^{-1}), suggests that females grow $\sim 33\%$ faster than males (Table 1).

3.4. Water temperature, timing and duration of spawning and maturation

The mean monthly water temperature at the bottom of the water column in the lower reaches of the SCE, where most *A. pflaumii* were collected (Poh et al., 2019) was 16°C in July, before increasing progressively to 18°C in October and again to 25°C in February, before declining rapidly to 16°C in June (Fig. 5a).

Mean monthly GSI's for female *A. pflaumii* rose sharply from 1.0 in September to >4.2 in October, November and February, before abruptly decreasing to 1.3 in March and remaining low (<3.0) between April and June (Fig. 5b). The trend in mean monthly GSI's for males was similar to that for females, but less pronounced; increasing steadily between August and November, attaining a maximum value in February (1.1), then declining rapidly to 0.2 in March and remaining low through to June (Fig. 5c).

In July, female *A. pflaumii* possessed stage II (immature/resting) and III/IV (developing/maturing) ovaries. Of the three females caught in August, two possessed stage IV ovaries (maturing) and the other possessed stage V/VI (mature/spawning) ovaries (Fig. 6a). Female *A. pflaumii* with stage III/IV and V/VI

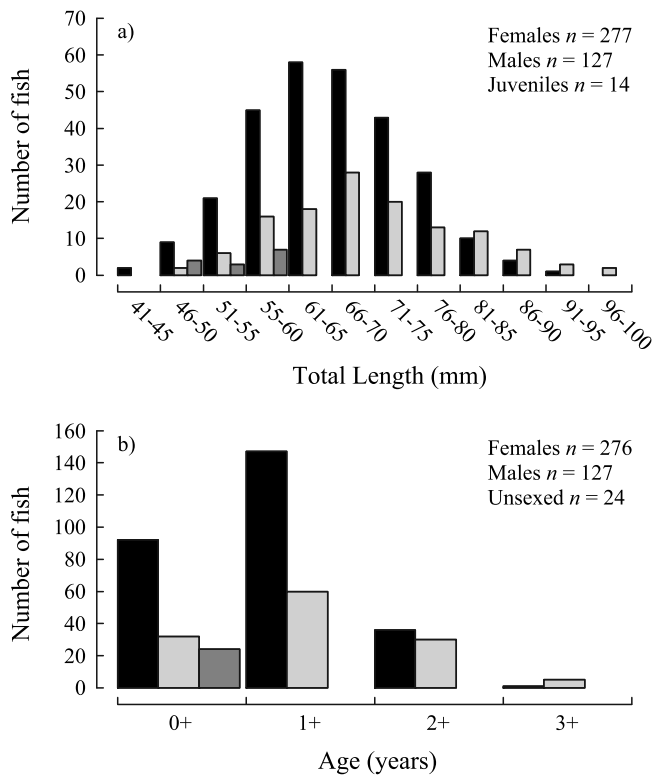


Fig. 3. (a) Length and (b) age frequency distributions for female (black bars), male (grey bars) and unsexed (dark grey bars) *Acentrogobius pflaumii* from the Swan-Canning Estuary.

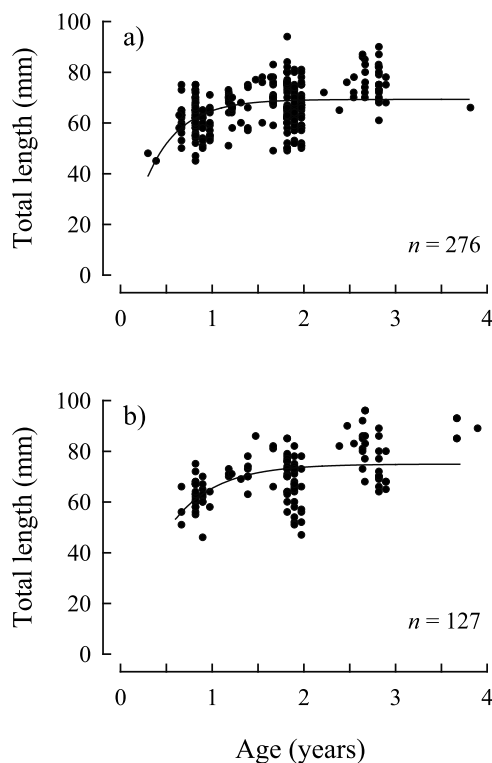


Fig. 4. Von Bertalanffy growth curves, with t_0 constrained to 0.08 years, fitted to the individual lengths at age of (a) female and (b) male *Acentrogobius pflaumii* in the Swan-Canning Estuary.

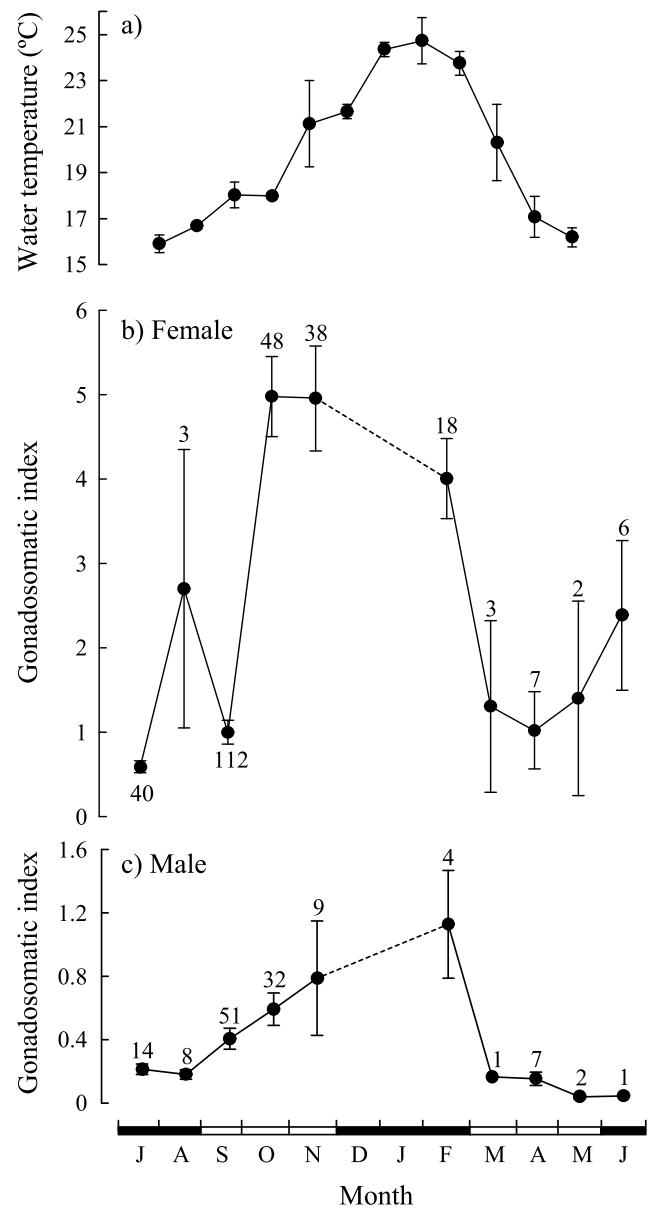


Fig. 5. Mean monthly (a) water temperature (± 1 SE) at the bottom of the water column and gonadosomatic indices (± 1 SE) for (b) female and (c) male *Acentrogobius pflaumii* in the Swan-Canning Estuary. On the x-axis closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months.

ovaries were present between August and November, and also in February. The frequency of females with stage V/VI ovaries was highest in October (~67%), November (~42%) and February (~61%). Females with stage VII/VIII (spent/recovering spent) ovaries were first recorded in March and occurred through to April (Fig. 6a). Females with stage V/VI ovaries are present until May, while those with stage II and III/IV ovaries were present in June (Fig. 6a). The prevalence of the different stages of testes among months for male *A. pflaumii* were similar to those for the ovaries of females, with an increasing frequency in the occurrence of stage III/IV testes between July and September and an increasing occurrence of stage V/VI testes between September and November (Fig. 6b).

The prevalence of female and male *A. pflaumii* with gonads at different stages of development, particularly those between July and November, indicate that all females and males, within

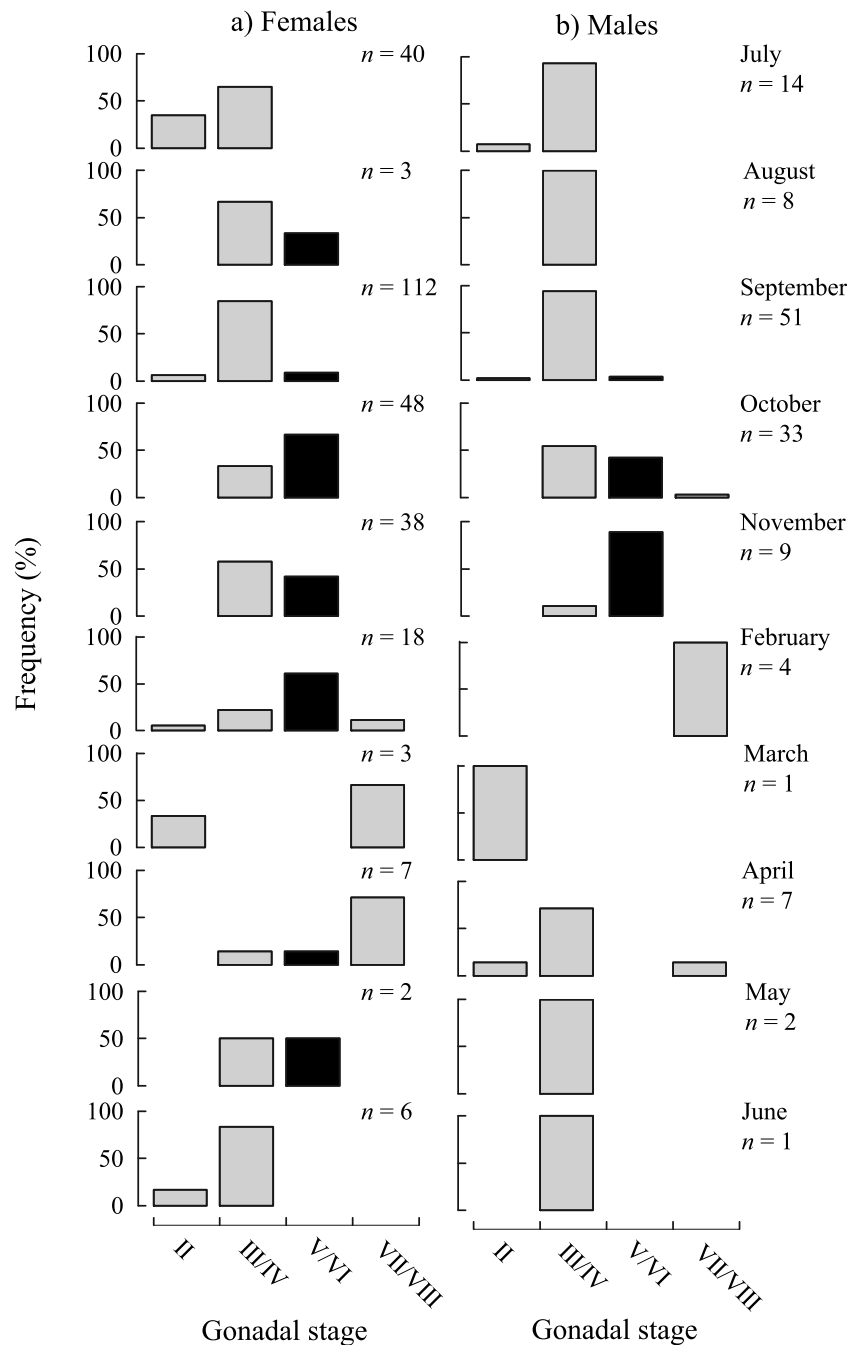


Fig. 6. Monthly percentage frequencies of occurrence of gonadal stages in (a) female and (b) male *Acentrogobius pflaumii* in the Swan-Canning Estuary. Black histograms represent stage V/VI (mature/spawning) gonads.

the length ranges sampled, progress through to maturity. This is consistent with the fact that during the main spawning period of October to February, all females and males possessed gonads at stages III/IV to VII/VIII (Fig. 6). All males and all but one female caught during the peak spawning period of October to February possessed mature gonads (stages III/VI–VII/VIII). Thus, all fish with ages and lengths > 10 months and 45 mm, respectively, were mature.

3.5. Oocyte diameter frequency distributions

The oocyte diameter frequencies for mature ovaries (stage V) from five female *A. pflaumii* caught during the spawning period,

ranged in length from 67–85 μm and were conspicuously discontinuous (Fig. 7). Thus, previtellogenic oocytes (i.e. chromatin nucleolar and perinucleolar oocytes) in the ovary of each female produced a prominent modal class of 41–100 μm , while yolk granule stage oocytes ranged in diameter from 321–480 μm (Fig. 7).

4. Discussion

This study was undertaken to determine the growth rates and reproductive biology of the non-indigenous gobiid *A. pflaumii* in the warm-temperate SCE and elucidate whether this species is able to spawn in the estuary and, if so, the timing and duration of spawning and the length and ages at maturity for females

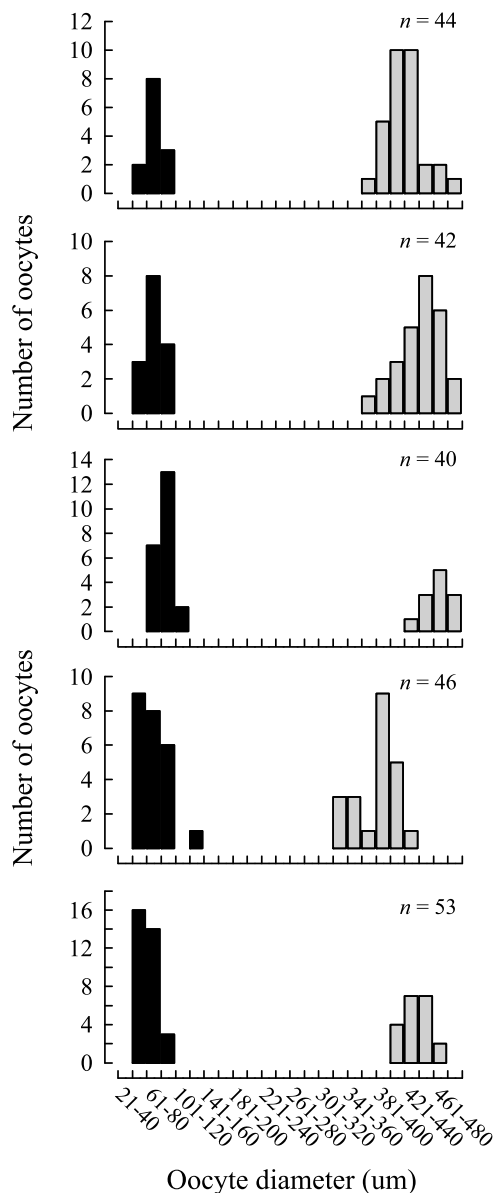


Fig. 7. Oocyte diameter frequency distributions for ovaries of five mature/spawning (stage V/VI) *Acentrogobius pflaumii* in the Swan-Canning Estuary. Previtellogenic (i.e. chromatin nucleolar and perinucleolar) oocytes, black bars; Yolk granule stage oocytes, grey bars. n = number of oocytes measured.

and males. These data were then compared with available data for this species in its cooler native environments and to those for native species of gobiid in the SCE. The results provide an understanding of the plasticity of the biological characteristics of *A. pflaumii*, and fundamental information for evaluating the risk that this invasive species poses to the native faunal communities and the ecological functioning of the SCE and potentially other estuaries in southwestern Australia.

4.1. Age validation, length and age composition and growth

The marginal increments for otoliths of *A. pflaumii* with 1 and 2–3 opaque zones exhibited a significant increase throughout April to June, followed by a substantial decrease, suggesting that opaque zones become delineated during July and thus the new translucent zone begins forming during mid- to late winter (July–August). This is somewhat atypical, as opaque zones

in the otoliths of most fish species in southwestern Australia become delineated in late spring to early summer, e.g. *Sillago schomburgkii*, *Acanthopagrus butcheri* and *Platycephalus westraliae* (Hyndes and Potter, 1997; Sarre and Potter, 2000; Coulson et al., 2017). The use of marginal increment analysis to validate growth zones formation is consistent with the results for other gobiids (Gumus and Kurt, 2009; Sokołowska and Fey, 2011; Hajji et al., 2013).

In the SCE ($\sim 32^\circ\text{S}$), female and male *A. pflaumii* attain maximum lengths of 94 and 96 mm, respectively, which is much larger than the corresponding values of 72 mm and ~ 50 mm (standard length) in its native habitats of Gwangyang Bay, South Korea ($\sim 34^\circ\text{N}$), and Wakasa Bay, Japan ($\sim 35^\circ\text{N}$), respectively, and 75 mm in New Zealand ($\sim 37^\circ\text{S}$), where *A. pflaumii* is also a non-indigenous species (Masuda et al., 1984; Francis et al., 2003; Baeck et al., 2004). As the water temperature of Gwangyang Bay drops to $\sim 5^\circ\text{C}$ in winter months (Lee and Kang, 2010), it is assumed that the large proportion of growth occurs over a very short period. The longer growing season for *A. pflaumii* in the SCE afforded by water temperatures remaining much higher for a far longer period, are suggested to have contributed to *A. pflaumii* attaining a greater maximum size compared to other cooler regions. However, in Wakasa Bay, Japan, at $\sim 35^\circ\text{N}$, where water temperatures are similar to that experienced in the SCE, falling to $\sim 10^\circ\text{C}$ in winter and rising to almost 30°C in summer, *A. pflaumii* only attains a standard length of ~ 50 mm (Matsui et al., 2014).

The large variation in the lengths at age recorded for female and male *A. pflaumii* in the SCE can, in part, be attributed to the fact that this species is capable of spawning over an extended period, resulting in individuals within the same cohort commencing life and growth when environmental conditions are very different. For example, individuals spawned in late winter and early spring (i.e. August–September) will have the entire following spring and summer in which to grow before entering the next winter, whilst those spawned in late summer (i.e. February), have only a few months of warmer conditions in which to grow before entering winter. In the SCE, the native *P. olorum* exhibits a biannual spawning period that results in divergent patterns of growth in this species since individuals within the same age cohort may be up to 9 months apart (Gill et al., 1996). Protracted spawning in *Neogobius melanostomus* resulted in individuals of the 0+ cohort that were spawned in late spring attaining a size of 111 mm in one year, compared to only 42 mm for those spawned in mid-summer (Shemonaev and Kirilenko, 2009).

The growth curves for *A. pflaumii* in the SCE indicate that, on average, males obtained a larger size than females, whereas, females exhibited faster relative growth. Sex-based differences in growth and size have been noted in several gobiid species and are attributed to differences in the cost of gamete production, parental care, mating systems and sexual selection (Hernaman and Munday, 2005). The larger maximum sizes displayed by male *A. pflaumii* are a typical feature of most gobiid species, such as the *Aphia minuta*, *Zosterisessor ophiocephalus* and *N. melanostomus* (La Mesa, 1999; Gumus and Kurt, 2009; Hajji et al., 2013). As gobiids are typically polygynous, the larger size attained by males is thought to aid in attracting multiple female mates and in parental care activities, such as guarding and fanning nests (Miller, 1984; Lindström and Hellström, 1993; Hernaman and Munday, 2005).

4.2. Habitat

In the SCE, *A. pflaumii*, which were all >40 mm, constituted 47% of the gobiid fauna in the offshore, deeper, waters and was essentially restricted to the lower “marine” region of the estuary (Hogan-West et al., 2019). However, the same fishing

gear that caught these larger individuals did not catch any *A. pflaumii* <40 mm, suggesting that, either the sampling method was not able to catch fish of this size, or that small individuals are not present in the lower reaches of the SCE. As the otter trawl, however, did catch other small benthic fish and prawns (i.e. <40 mm total length), and hand trawling in shallow waters did not catch any *A. pflaumii* (Poh et al., 2019; Hogan-West et al., 2019), the small individuals probably were not present in the habitat sampled during this study. The deep waters of the lower SCE possesses very fine, silt-like, sediment, while sediment grain size in shallow waters is much coarser (Tweedley et al., 2017). Tank trials and field studies of morphs of *A. pflaumii* (Suzuki et al., 2004) showed that there are strong sediment and depth preferences between the different morphs of this species (Horinouchi, 2008; Matsui et al., 2012).

The apparent absence of small *A. pflaumii* in the SCE parallels the findings of Francis et al. (2003), who did not catch small *A. pflaumii* from an established population in New Zealand. In contrast, surface and mid-water trawls, designed to sample larval fish, caught small *A. pflaumii* in the Jiulong River Estuary, China (Nan et al., 2009). Furthermore, the wide size range of *A. pflaumii* caught by Nan et al. (2009), suggests that *A. pflaumii* has a more mobile lifestyle than would be expected of a small-bodied, benthic fish. Therefore, this could potentially explain the absence of small *A. pflaumii* in the present study in which the sampling regime was solely designed to target the benthic species, particularly penaeids, within 1 m of the benthos, therefore potentially missing individuals higher in the water column. The lack of seagrass beds, a known settlement habitat of *A. pflaumii* (Horinouchi and Sano, 2000; Kanou et al., 2004) in the deeper waters of the SCE, and the existence of extensive seagrass beds just to the south in Cockburn Sound, where *A. pflaumii* was first identified (Maddern and Morrison, 2009), indicate that seagrass may provide suitable habitat for the early juveniles of *A. pflaumii*. The unpublished data of M. Horinouchi (cited in Horinouchi, 2007), indicated that the abundance of juvenile *Acentrogobius* species were influenced by the availability of symbiotic shrimp burrows, which in some areas were more common in seagrass beds, but were also present in bare sand areas. Thus, to more accurately describe the growth of *A. pflaumii* throughout their life and, in particular, during their juvenile stage, methods that sample fishes in the water column and in seagrass beds, may need to be considered.

4.3. Time and duration of spawning

The trends exhibited by the GSI's and prevalence of fish with mature and spawning gonads (stage V/VI), particularly females, demonstrate that *A. pflaumii* is capable of spawning in the SCE over 10 months of the year from late winter (August) to late autumn (May). However, the high prevalence of females with mature and spawning ovaries (stage V/VI) in November, December and February, as well as the first occurrence of females with spent and recovering ovaries (stage VII/VIII) in February indicate that spawning takes place mainly between November (mid-spring) and February (late summer). In its native habitat of Gwangyang Bay, South Korea, *A. pflaumii* spawns during a similar seasonal time period, albeit more restricted, from April (early spring) to June (early summer), as does the confamilial as does *Favonigobius gymnauchen* in Korean waters (Lee et al., 2000; Baeck et al., 2004). The shorter spawning duration in Gwangyang Bay likely reflects the fact that water temperature drops to as low as ~5 °C during the winter months (Lee and Kang, 2010), compared to 16 °C in the SCE. By commencing and ceasing spawning when water temperatures are increasing in Gwangyang Bay, *A. pflaumii* are providing their larvae with the longest possible period

of warm conditions in which to commence life. In contrast, as water temperatures remain higher throughout the year in the SCE, *A. pflaumii* is able to spawn over a more protracted period. *Neogobius fluviatilis* also exhibited a more protracted spawning period in its invaded environment in the lower Rhine, Germany, in comparison to its native habitat of the Danube, Bulgaria (c.f. Konečná and Jurajda, 2012; Gertzen et al., 2016). Despite water temperature in Wakasa Bay, Japan, falling to ~10 °C in winter and rising to ~30 °C in summer, and thus very similar to the SCE, the spawning period of *A. pflaumii* in Wakasa Bay is more restricted, occurring from April (early spring) to August (late summer) (Matsui et al., 2014). In Wakasa Bay, however, *A. pflaumii* co-occurs with two other sympatric species, with the spawning period for the other two species peaking in June and July (Matsui et al., 2014). The shorter spawning period of *A. pflaumii* in Wakasa Bay, in comparison to the SCE, is hypothesised to be related to the competition between sympatric species, in particular the food resource requirements, which are known to be similar between the three species (Horinouchi, 2008).

The timing of the main spawning period displayed by *A. pflaumii* in the SCE is also consistent with the native gobiid *P. olorum* and other estuarine species in this estuary, such as *Leptatherina presbyteroides*, *Craterocephalus mugiloides*, *Leptatherina wallacei*, *Ostorhinchus rueppelli*, *Acanthopagrus butcheri*, *Amniataba caudavittata* and *P. westraliae* (Prince and Potter, 1983; Chrystal et al., 1985; Potter et al., 1994; Gill et al., 1996; Sarre and Potter, 1999; Coulson et al., 2017). Fish species of southwestern Australian estuaries typically spawn during late spring and summer as the conditions during this time, i.e. limited tidal action and negligible freshwater input and relatively high salinities, provide a very stable, benign environment conducive to spawning and, presumably, the retention, growth and survival of eggs and larvae (Potter and Hyndes, 1999; Potter et al., 2015b).

The maximum mean monthly GSI for female *A. pflaumii* in the SCE is approximately four times greater than that of their males. The large differences in the mass of the ovaries and testes suggest that this species spawns in pairs, a common reproductive strategy employed by gobiids (e.g. Hernaman and Munday, 2005). The reduction in energy allocated to reproduction in male gobiids is thought to stem from a reduced requirement for sperm due to increased fertilisation rates that accompany pair spawning and laying eggs in nests compared with broadcast spawning. For example, male *N. melanosomus* successfully fertilise ~95% of the >10,000 eggs that can be laid in the nest (Charlebois et al., 1997). It should also be noted that in South Korea, female *A. pflaumii* exhibited a much higher maximum mean GSI value of 13.8% during peak spawning times (Baek et al., 2004). This suggests that the lower GSIs for *A. pflaumii* in the SCE may be compensated for by a longer spawning period, while the shorter spawning period in South Korea is compensated for by greater spawning intensity during that period. In *Pomacentrus coelestis*, spawning intervals were shortest and clutch mass greatest in high latitude populations (Kokita, 2004), while *Solea solea* in colder North Atlantic waters possessed higher rates of reproductive investment than those in more southern, warmer waters (Mollet et al., 2013).

5. Conclusion

The gobiid *Acentrogobius pflaumii* is native to East Asia, but through ship ballast water, has been found well outside its native range, including in southwestern Australia. This study has shown that the biological traits of the population of *A. pflaumii* in the SCE, such as rapid growth, early maturation and an extended spawned period, are likely to have aided in the successful colonisation of this species in environments outside its native distribution. This biological information provides further evidence and understanding of the phenotypic plasticity that non-native species possess

in order to make them successful colonisers of habitats outside their typical range and may assist managers in identifying the risk that they pose to other environments within their jurisdiction and contribute to invasion risk assessments (Kornis et al., 2017; Karakuş et al., 2018).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Baech, G.W., Kim, J.W., Huh, S.H., 2004. Maturation and spawning of striped goby (*Acentrogobius pflaumi*) (Teleostei: Gobiidae) collected in the Gwangyang Bay, Korea. *Korean J. Fish. Aquat. Sci.* 37, 226–231.
- Beatty, S.J., Allen, M.G., Whitty, J.M., Lymbery, A.J., Keleher, J.J., Tweedley, J.R., Ebner, B.C., Morgan, D.L., 2017. First evidence of spawning migration by goldfish (*Carassius auratus*): implications for control of a globally invasive species. *Ecol. Freshw. Fish.* 26, 444–455.
- Broadley, A.D., Tweedley, J.R., Loneragan, N.R., 2017. Estimating biological parameters for potential penaeid restocking in a temperate estuary. *Fish. Res.* 186, 488–501.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish. Biol.* 59, 197–242.
- Carlton, J.T., 1996. Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.* 78, 97–106.
- Carlton, J.T., Reid, D.M., van Leeuwen, H., 1995. The role of shipping in the introduction of nonindigenous aquatic organisms to the coastal waters of the United States (other than the Great Lakes) and an analysis of control options. Report to US Coast Guard, Washington DC.
- Cerrato, R.M., 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47, 1416–1426.
- Chang, W.Y.B., 1982. A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.* 47, 1416–1426.
- Charlebois, P.M., Marsden, J.E., Goettel, R.G., Wolfe, R.K., Jude, D.J., Rudnik, S., 1997. The round goby, *Neogobius melanostomus* (Pallas). In: *A Review of European and North American Literature*. In: Illinois-Indiana Sea Grant Program and Illinois Natural History Survey, vol. 20, INHS Special Publication, p. 76.
- Chrystal, P.J., Potter, I.C., Loneragan, N.R., Holt, C.P., 1985. Age structure, growth rates, movement patterns and feeding in an estuarine population of the cardinalfish *Apogon rueppellii*. *Mar. Biol.* 85, 185–197.
- Coulson, P.G., Hall, N.G., Potter, I.C., 2016. Biological characteristics of three co-occurring species of armorhead from different genera vary markedly from previous results for the Pentacerotidae. *J. Fish. Biol.* 89, 1393–1418.
- Coulson, P.G., Hall, N.G., Potter, I.C., 2017. Variations in biological characteristics of temperate gonochoristic species of platycephalidae and their implications: A review. *Estuar. Coast. Mar. Sci.* 190, 50–68.
- Davidson, A.M., Jennions, M., Nicotra, A.B., 2011. Do invasive species show higher phenotypic plasticity than native species and if, is it adaptive? A meta-analysis. *Ecol. Lett.* 14, 419–431.
- Depczynski, M., Bellwood, D.R., 2005. Shortest recorded vertebrate lifespan found in a coral reef fish. *Curr. Biol.* 15, 288–289.
- Depczynski, M., Bellwood, D.R., 2006. Extremes, plasticity, and invariance in vertebrate life history traits: insights from coral reef fishes. *Ecol.* 87, 3119–3127.
- Francis, M.P., Walsh, C., Morrison, M.A., Middleton, C., 2003. Invasion of the Asian goby, *Acentrogobius pflaumi*, into New Zealand, with new locality records of the introduced bridled goby, *Arenigobius bifrenatus*. *New Zeal. J. Mar. Freshw. Res.* 37, 105–112.
- Fricke, R., Eschmeyer, W.N., Fong, J.D., 2019. Eschmeyer's catalog of fishes. (Online Database <http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>) accessed 19 September 2019.
- Gertzen, S., Fidler, A., Kreische, F., Kwabek, L., Schwamborn, V., Borcherdig, J., 2016. Reproductive strategies of three invasive Gobiidae co-occurring in the Lower Rhine (Germany). *Limnologia* 56, 39–48.
- Gill, H.S., Potter, I.C., 1993. Spatial segregation amongst goby species within an Australian estuary, with a comparison of the diets and salinity tolerance of the two most abundant species. *Mar. Biol.* 117, 515–526.
- Gill, H.S., Wise, B.S., Potter, I.C., Chaplin, J.A., 1996. Biannual spawning periods and resultant divergent patterns of growth in the estuarine goby *Pseudogobius olorum*: Temperature induced? *Mar. Biol.* 125, 453–466.
- Gomon, M.F., Bray, D.J., Kuiter, R.H., 2008. *Fishes of Australia's Southern Coast*. New Holland, Sydney.
- Gumus, A., Kurt, A., 2009. Age structure and growth by otolith interpretation of *Neogobius melanostomus* (Gobiidae) from Southern Black Sea. *Cybius* 33, 29–37.
- Hajji, F., Ouannes-ghorbel, A., Ghorbel, M., Jarbou, O., 2013. Age and growth of the grass goby *Zosterisessor ophiocephalus* Pallas, 1811 in the Gulf of Gabes (Tunisia, Central Mediterranean). *Acta Adriat.* 54, 27–40.
- Hempel, M., Magath, V., Neukamm, R., Thiel, R., 2018. Feeding ecology, growth and reproductive biology of round goby *Neogobius melanostomus* (Pallas, 1814) in the brackish Kiel Canal. *Mar. Biodivers.* 49, 795–807.
- Hernaman, V., Munday, P.L., 2005. Life-history characteristics of coral reef gobies. I. Growth and life-span. *Mar. Ecol. Prog. Ser.* 290, 207–221.
- Hernaman, V., Munday, P.L., Schlappy, M.L., 2000. Validation of otolith growth-increment periodicity in tropical gobies. *Mar. Biol.* 137, 715–726.
- Hewitt, C.L., Campbell, M.L., Thresher, R.E., Martin, R.B., Boyd, S., Cohen, B.F., Currie, D.R., Gomon, M.F., Keough, M.J., Lewis, J.A., Lockett, M.M., 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar. Biol.* 144, 183–202.
- Hogan-West, K., Tweedley, J.R., Coulson, P.G., Poh, B., Loneragan, N.R., 2019. Abundance and distribution of the non-indigenous *Acentrogobius pflaumi* and native gobiids in a temperate Australian estuary. *Estuaries Coast.* 42, 1612–1631.
- Horinouchi, M., 2007. Distribution patterns of benthic juvenile gobies in and around seagrass habitats: effectiveness of seagrass shelter against predators. *Estuar. Coast. Shelf Sci.* 72, 657–664.
- Horinouchi, M., 2008. Patterns of food and microhabitat resource use by two benthic gobiid fishes. *Environ. Biol. Fishes* 82, 187–194.
- Horinouchi, M., Sano, M., 2000. Food habits of fishes in a *Zostera marina* bed at Aburatsubo, central Japan. *Ichthyol. Res.* 47, 163–173.
- Hunter, J.R., Macewicz, B.J., 1985. Measurement of spawning frequency in multiple spawning fishes. In: Lasker, R. (Ed.), *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fishes: Application to the Northern Anchovy, Engraulis mordax*. NOAA Technical Report, National Marine Fisheries Service, NMFS 36, Springfield, VA, pp. 79–94.
- Hyndes, G.A., Potter, I.C., 1997. Age, growth and reproduction of *Sillago schomburgkii* in southwestern Australian nearshore waters and comparisons of life history styles of a suite of *Sillago* species. *Environ. Biol. Fish.* 49, 435–447.
- Iglesias, M., Brothers, E.B., Morales-Nin, B., 1997. Validation of daily increment deposition in otoliths. age and growth determination of *Aphia minuta* (Pisces: Gobiidae) from the northwest Mediterranean. *Mar. Biol.* 129, 279–287.
- Iida, M., Watanabe, S., Tsukamoto, K., 2010. Validation of otolith daily increments in the amphidromous goby *Sicyopterus japonicus*. *Coast. Mar. Sci.* 34, 39–41.
- Júza, T., Blabolil, P., Baran, R., Bartoň, D., Čech, M., Drašík, V., Frouzová, J., Holubová, M., Ketelaars, H.A., Kočvara, L., Kubečka, J., 2018. Collapse of the native ruffe (*Gymnocephalus cernua*) population in the Biesbosch lakes (the Netherlands) owing to round goby (*Neogobius melanostomus*) invasion. *Biol. Invasions* 20, 1523–1535.
- Kanou, K., Sano, M., Kohno, H., 2004. Food habits of fishes on unvegetated tidal mudflats in Tokyo Bay, central Japan. *Fish. Sci.* 70, 978–987.
- Karakuş, U., Top, N., Tepeköy, E.G., Britton, J.R., Tarkan, A.S., 2018. Life history characteristics of the potentially invasive Ponto-Caspian goby *Neogobius fluviatilis* in natural lakes from its native range (Black Sea region of Turkey). *Mar. Freshw. Res.* 69, 1544–1556.
- Kokita, T., 2004. Latitudinal compensation in female reproductive rate of a geographically widespread reef fish. *Environ. Biol. Fish.* 71, 213–224.
- Konečná, M., Jurajda, P., 2012. Population structure, condition, and reproduction characteristics of native monkey goby, *Neogobius fluviatilis* (Actinopterygii: Perciformes: Gobiidae), in the Bulgarian Danube. *Acta Ichthyol. Piscat.* 42, 321–327.

- Kornis, M.S., Weidel, B.C., Vander Zanden, M.J., 2017. Divergent life histories of invasive round gobies (*Neogobius melanostomus*) in Lake Michigan and its tributaries. *Ecol. Freshw. Fish.* 26, 563–574.
- Kovačić, M., 2006. Age structure, growth and mortality of the striped goby, *Gobius vittatus* (Gobiidae) in the northern Adriatic Sea. *Sci. Mar.* 70, 635–641.
- La Mesa, M., 1999. Age and growth of *Aphia minuta* (Pisces, Gobiidae) from the central Adriatic Sea. *Sci. Mar.* 63, 147–155.
- La Mesa, M., 2001. Age and growth of *Crystalllogobius linearis* (von Duben, 1845) (Teleostei : Gobiidae) from the Adriatic Sea. *Sci. Mar.* 65, 375–381.
- La Mesa, M., Arneri, E., Caputo, V., Iglesias, M., 2005. The transparent goby, *Aphia minuta*. Review of biology and fisheries of a paedomorphic European fish. *Rev. Fish. Biol. Fish.* 15, 89–109.
- Laevastu, T., 1965. Manual of Methods in Fisheries Biology. FAO, Rome.
- Lee, Y.S., Kang, C.K., 2010. Causes of COD increases in Gwangyang Bay, South Korea. *J. Environ. Monitor.* 12, 1537–1546.
- Lee, J.S., Kim, J.W., Kang, J.C., Shin, Y.K., Chin, P., 2000. Reproductive cycle and gonadal development of the naked-headed Goby, *Favonigobius gymnauchen* (Teleostei: Gobiidae). *Korean J. Fish. Aquat. Sci.* 33, 219–224.
- Lindström, K., Hellström, M., 1993. Male size and parental care in the sand goby, *Pomatoschistus minutus*. *Ethol. Ecol. Evol.* 5, 97–106.
- Lockett, M.M., Gomon, M.F., 2001. Ship mediated fish invasions in Australia: Two new introductions and a consideration of two previous invasions. *Biol. Invasions* 3, 187–192.
- Loneragan, N.R., Potter, I.C., Lenanton, R.C.J., 1989. Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Mar. Biol.* 103, 461–479.
- Loneragan, N.R., Potter, I.C., Lenanton, R.C.J., Caputi, N., 1986. Spatial and seasonal differences in the fish fauna of the shallows in a large Australian estuary. *Mar. Biol.* 92, 575–586.
- Maddern, M.G., Morrison, S., 2009. Introduction of the Streaked Goby *Acentrogobius pflaumii* (Bleeker 1853) (Pisces: Gobiidae) into south-western Australia. *Aust. Zool.* 35, 96–99.
- Masuda, H., Amaoka, K., Araga, C., Uyeno, T., Yoshino, T., 1984. The Fishes of the Japanese Archipelago. Tokai University press, Japan.
- Matsui, S., Inui, R., Yamashita, Y., 2012. Distribution and habitat use of three *Acentrogobius* (Perciformes: Gobiidae) species in the coastal waters of Japan. *Ichthyol. Res.* 59, 373–377.
- Matsui, S., Ueno, M., Yamashita, Y., 2014. Growth characteristics and reproductive biology of three sympatric *Acentrogobius* (Perciformes: Gobiidae) species in Maizuru Bay, Kyoto Prefecture. *Bull. Jpn. Soc. Fish. Oceanogr.* 78, 75–85.
- Mazzoldi, C., Rasotto, M.B., 2001. Extended breeding season in the marbled goby, *Pomatoschistus marmoratus* (Teleostei: Gobiidae), in the Venetian Lagoon. *Environ. Biol. Fish.* 61, 175–183.
- Mead-Hunter, D., 2005. Another introduced fish species for Western Australian waters. *West. Aust. Nat.* 24, 204.
- Miller, P.J., 1984. The tokology of gobioid fishes. In: Potts, G.W., Wotton, R.J. (Eds.), *Fish Reproduction: Strategies and Tactics*. Academic Press, Orlando, pp. 119–153.
- Mollet, F.M., Engelhard, G.H., Vainikka, A., Laugen, A.T., Rijnsdorp, A.D., Ernande, B., 2013. Spatial variation in growth, maturation schedules and reproductive investment of female sole *Solea solea* in the Northeast Atlantic. *J. Sea Res.* 84, 109–121.
- Nan, L.N., Changchun, S., Junsheng, Z., 2009. Species composition and seasonal variation of fish larvae and juveniles in Jiulong River estuary. *South China Fish. Sci.* 5, 1–8.
- Nelson, G.A.N., 2015. Fishmethods: fishery science methods and models in R. R package version 1.9-0. Available at: <https://CRAN.R-project.org/package=fishmethods> (accessed 9 December 2015).
- Okamura, H., Semba, Y., 2009. A novel statistical method for validating the periodicity of vertebral growth band formation in elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 66, 771–780.
- Pellicice, F.M., Latini, J.D., Agostinho, A.A., 2015. Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. *Hydrobiologia* 746, 271–283.
- Poh, B., Tweedley, J.R., Chaplin, J.A., Trayler, K.M., Crisp, J.A., Loneragan, N.R., 2019. Influence of physico-chemical and biotic factors on the distribution of a penaed in a temperate estuary. *Estuar. Coast. Mar. Sci.* 218, 70–85.
- Potter, I.C., Hyndes, G.A., 1999. Characteristics of the ichthyofaunas of south-western Australian estuaries, including comparisons with holarctic estuaries and estuaries elsewhere in temperate Australia: A review. *Austral. Ecol.* 24, 395–421.
- Potter, I.C., Neira, F.J., Wise, B.S., Wallace, J.H., 1994. Reproductive biology and larval development of the terapontid *Amniataba caudavittata*, including comparisons with the reproductive strategies of other estuarine teleosts in temperate Western Australia. *J. Fish Biol.* 45, 57–74.
- Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015a. The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish. Fish.* 16, 230–239.
- Potter, I.C., Veale, L., Tweedley, J.R., Clarke, K.R., 2016. Decadal changes in the ichthyofauna of a eutrophic estuary following a remedial engineering modification and subsequent environmental shifts. *Estuar. Coast. Mar. Sci.* 181, 345–363.
- Potter, I.C., Warwick, R.M., Hall, N.G., Tweedley, J.R., 2015b. The physico-chemical characteristics, biota and fisheries of estuaries. In: Craig, J. (Ed.), *Freshwater Fisheries Ecology*. Wiley-Blackwell, pp. 48–79.
- Prince, J.D., Potter, I.C., 1983. Life-cycle duration, growth and spawning times of five species of atherinidae (Teleostei) found in a Western Australian estuary. *Mar. Freshw. Res.* 34, 287–301.
- Randall, J.E., Delbeek, J.C., 2009. Comments on the extremes in longevity in fishes, with special reference to the Gobiidae. *Proc. Calif. Acad. Sci.* 60, 447–454.
- Ruiz, G., Carlton, J., Grosholz, E., Hines, A., 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *Am. Zool.* 37, 621–632.
- Sarre, G.A., Potter, I.C., 1999. Comparisons between the reproductive biology of black bream *Acanthopagrus butcheri* (Teleostei: Sparidae) in four estuaries with widely differing characteristics. *Int. J. Salt Lake Res.* 8, 179–210.
- Sarre, G.A., Potter, I.C., 2000. Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors. *Fish. Bull.* 98, 78–799.
- Shao, K.T., Chen, J.P., Kao, P.H., Wu, C.Y., 1993. Fish fauna and their geographical distribution along the western coast of Taiwan. *Acta. Zool. Taiwanica* 4, 113–140.
- Shemonaev, E.V., Kirilenko, E.V., 2009. Features of biology of the round goby *Neogobius melanostomus* (Perciformes, Gobiidae) in waters of Kuibyshev Reservoir. *J. Ichthyol.* 49, 454–459.
- Sokolowska, E., Fey, D.P., 2011. Age and growth of the round goby *Neogobius melanostomus* in the Gulf of Gdańsk several years after invasion. Is the Baltic Sea a new Promised Land? *J. Fish Biol.* 78, 1993–2009.
- Suzuki, T., Shibukawa, K., Yano, K., 2004. *Acentrogobius* sp. A, *Acentrogobius* sp. B and *Acentrogobius* sp. C. In: Senou, H. (Ed.), *A photographic Guide to the Gobioid Fishes of Japan*. Japanese Text and Plates. Heibonsha Press, Tokyo, pp. 416–418.
- Thresher, R.E., 1999. Diversity, impacts and options for managing invasive marine species in Australian waters. *Australas. J. Env. Man.* 6, 137–148.
- Tweedley, J.R., Loneragan, N.R., Crisp, J.A., Poh, B., Broadley, A.D., Bennett, A.L., Hodson, K.P., Trayler, K.M., Jenkins, G.I., Chaplin, J.A., 2017. Stock Enhancement of the Western School Prawn (*Metapenaeus dalli*) in the Swan-Canning Estuary; Evaluating Recruitment Limitation, Environment and Release Strategies. Report for the Fisheries Research and Development Corporation, Murdoch University, Perth, Western Australia, p. 546.
- Tweedley, J.R., Warwick, R.M., Potter, I.C., 2016. The contrasting ecology of temperate macrotidal and microtidal estuaries. *Oceanogr. Mar. Biol.:Annu. Rev.* 54, 73–171.
- Valesini, F.J., Cottingham, A., Hallett, C.S., Clarke, K.R., 2017. Interdecadal changes in the community, population and individual levels of the fish fauna of an extensively modified estuary. *J. Fish Biol.* 90, 1734–1767.
- Winterbottom, R., Alofs, K.M., Marseu, A., 2011. Life span, growth and mortality in the western Pacific goby *Trimma benjamini*, and comparisons with *t. nasa*. *Environ. Biol. Fish.* 91, 295–301.
- Wonham, M.J., Carlton, J.T., Ruiz, G.M., Smith, L.D., 2000. Fish and ships: relating dispersal frequency to success in biological invasions. *Mar. Biol.* 136, 1111–1121.