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# **Biology of a marine estuarine-opportunist fish species in a microtidal estuary, including comparisons among decades and with coastal waters**

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## **Abstract**

The biological characteristics of a marine and macrophyte-associated species (*Pelates octolineatus*) in a large microtidal, eutrophic estuary in 2008–10 were determined. Comparisons are made with those of individuals remaining in coastal waters and during two earlier periods in the estuary when plant biomass differed markedly. *P. octolineatus* start entering the Peel–Harvey Estuary in mid-summer, soon after metamorphosis, with many remaining there until autumn when they are ~15 months old. These individuals, and older fish that re-entered the estuary in summer, then return to the sea where they spawn from late spring to early summer. Most *P. octolineatus* in the estuary were less than or equal to the length at maturity and all were <4 years old, whereas individuals up to 10 years old were caught in coastal embayments, emphasising that the estuary acts mainly as a nursery for this terapontid. Growth in the estuary was seasonal and peaked earlier and was greater than in marine waters. Abundance of *P. octolineatus* in the estuary was greater in 2008–10 and 1980–81 than in 1996–97, when macrophytes were less abundant. The results demonstrate how a marine estuarine-

opportunists can benefit from using both estuaries and coastal waters as a nursery area and capitalise on variations in environmental conditions.

**Additional keywords:** eutrophication, population dynamics, reproductive biology, recruitment, seasonal growth.

## Introduction

The fish faunas of estuaries in temperate regions of the northern and southern hemispheres are dominated by marine taxa, both in terms of species richness and abundance (e.g. Haedrich 1983; Potter *et al.* 1990; Elliott and Dewailly 1995; Able and Fahay 2010). As many of those species enter estuaries regularly and in substantial numbers they have been termed marine estuarine-opportunists (Potter and Hyndes 1999; Able 2005; Franco *et al.* 2008; Potter *et al.* 2015). Furthermore, as marine estuarine-opportunists typically enter these systems mainly during juvenile life, estuaries constitute important nursery areas for those species (Blaber and Blaber 1980; Claridge *et al.* 1986; Maes *et al.* 2005). The juveniles of many marine estuarine-opportunists often remain; however, in the marine environment and use protected nearshore coastal waters as a nursery area (Valesini *et al.* 1997; Able and Fahay 2010).

It has been proposed that the high productivity of estuaries (Schelske and Odum 1961; Whittaker and Likens 1975; Mann 1982; Heip *et al.* 1995) enables the juveniles of marine estuarine-opportunists to grow faster than in their less productive natal marine environment and thereby attain more rapidly a size that reduces their susceptibility to predation (Kennish 1990; Potter and Hyndes 1999). Thus, the juveniles of the common sole (*Solea solea*) in France and the stone flounder (*Platichthyes bicoloratus*) in Japan have been shown to grow faster in estuarine than nearshore coastal waters (Le Pape *et al.* 2003; Yamashita *et al.* 2003). In contrast, no differences were found between the growth of five species in estuaries and on the inner continental shelf on the temperate east coast of North America (Woodland *et al.* 2012). Results of the few comparisons between growth in the coastal marine and estuarine environments in the northern hemisphere thus differ, and there have been no

quantitative comparisons of the growth of a marine estuarine-opportunist species in the main body of an estuary in the southern hemisphere with that of those individuals of the same species which remained in their natal coastal waters.

Following an extensive review of the literature, Gillanders *et al.* (2003) concluded that marine species spend from 8 days to 5 years in their juvenile habitats, which include coastal waters, surf zones and estuaries. The juveniles of various species of marine estuarine-opportunist often enter macrotidal estuaries for a relatively short period each year, with their movements into and out of these systems varying among those species in a sequential time-staggered manner (e.g. Claridge *et al.* 1986; Potter *et al.* 2001; Thiel *et al.* 2003; Maes *et al.* 2005). Numerous marine estuarine-opportunist species also enter microtidal systems early in life and frequently remain there for many months and sometimes years (Chubb *et al.* 1981; Potter *et al.* 1988; Able and Fahay 2010).

In coastal marine waters on the temperate and microtidal lower west coast of Australia, many western striped grunter (*Pelates octolineatus*) spend their first year of life in dense, nearshore seagrass meadows in embayments and then move out into deeper offshore waters where seagrass is less dense (Veale *et al.* 2015). They typically become mature 1 year later. *P. octolineatus* is, however, a classic marine estuarine-opportunist because, like several other species on the same coast, substantial numbers of its juveniles also enter estuaries and remain there throughout the year (Potter *et al.* 1983; Loneragan *et al.* 1986; Veale *et al.* 2015). In terms of habitat, it is particularly noteworthy that, during extensive sampling of habitats in nearshore waters on the lower west coast of Australia, 0+ *P. octolineatus* was only found to be abundant in seagrass (Valesini *et al.* 2004). Furthermore, this species was the most abundant teleost found in seagrass meadows in a large subtropical embayment in the mid-west coast of Australia (Burkholder *et al.* 2013). As with another terapontid, *Amniataba caudivittata*, on the lower-west coast of Australia (Wise *et al.* 1994), the growth of *P. octolineatus* in coastal marine waters is highly seasonal (Veale *et al.* 2015).

During the 1960s to early 1990s, the large Peel–Harvey Estuary on the lower-west coast of Australia became highly eutrophic, which was reflected in the production of massive macroalgal blooms (Birch 1982; McComb and Lukatelich 1995). This helps account for the weed-associated *P.*

*octolineatus* being the most abundant of the fish species caught during extensive sampling of this system during the 1980s (Potter *et al.* 1983; Loneragan *et al.* 1986). Although the *P. octolineatus* obtained during that period were not aged, length–frequency distributions demonstrated that large numbers of the 0+ age class of this marine estuarine-opportunist entered this system. Subsequently, a large and artificially constructed second entrance channel was opened into the Peel–Harvey Estuary in 1994 to increase the flushing of nutrients out of this system (McComb and Lukatelich 1995). The resultant substantial reductions in macroalgal biomass may thus account for the marked decline in the relative abundance of *P. octolineatus* in 1996–97 (Young and Potter 2003). Although the amount of macroalgae has increased and seagrass beds have developed in this estuary in recent years (Pedretti *et al.* 2011), it is not known whether these changes are reflected in increases in the abundance of this weed-associated species.

The aim of the current study was to collect sound quantitative data on the biological characteristics of *P. octolineatus* in the Peel–Harvey Estuary and compare these characteristics with those recorded for this species in the estuary in earlier decades and concomitantly in marine coastal waters. Such comparisons would demonstrate whether the abundance of this macrophyte-associated species is broadly related to the amount of plant material, and elucidate the functional roles played by estuaries and protected marine coastal waters in the life cycle of this marine estuarine-opportunist species. *P. octolineatus* was thus collected from throughout the Peel–Harvey Estuary in eight consecutive seasons in 2008–10 to assess whether the data are consistent with the following: (1) this marine terapontid enters the estuary early in life and remains there until it approaches the length and age at which maturity is attained in marine waters. The timing of emigration is considered in the context of the inter-related changes in freshwater discharge, salinity and water temperature and the trends exhibited by sequential stages in gonadal maturation; (2) the relative abundances of *P. octolineatus* in the Peel–Harvey Estuary were greater in 2008–10 and 1980–81 (Potter *et al.* 1983) than in 1995–1996 (Young and Potter 2003), when macrophytes were less prolific; and (3) the growth of *P. octolineatus* is greater in the more productive waters of the estuary than in protected marine coastal waters on the same coast.

## Materials and methods

### *Sampling regime*

*Pelates octolineatus* was sampled in the Mandurah Channel (MC), Peel Inlet and Harvey Estuary using 102.5 and 21.5 m-long seine nets (Fig. 1). For analyses, Peel Inlet was separated into western (WP) and eastern (EP) halves and the Harvey Estuary into northern (NH) and southern (SH) halves. Four sites in each of MC, WP, EP, NH and SH were sampled by both nets in the middle of each season between winter (July) 2008 and autumn (April) 2010, except for winter 2009, when sampling was restricted to three sites in each region because of adverse weather conditions. The regions nearest to the natural Mandurah and artificially constructed Dawesville entrance channels, i.e. WP and NH respectively, were also sampled using the 21.5-m seine net in the other 2 months of each of the above seasons and then monthly until summer (January) 2011. This provided additional length and age data for the regions where preliminary sampling had shown *P. octolineatus* to be most abundant. Salinity and water temperature at each site on each sampling occasion were measured in the middle of the water column using a Yellow Springs International Model 85 (YSI Incorporated, Yellow Springs, OH, USA) hand-held water quality meter.

The 102.5 m-long seine net, which comprised two 50 m-long wings of 25-mm mesh and a 2.5 m-long cod end of 9-mm mesh, swept an area of 1600 m<sup>2</sup>. The 21.5 m-long seine net, which was 1.5 m high and consisted of two 10 m-long wings of 9-mm mesh and a 1.5-m bunt of 3-mm mesh, swept an area of 116 m<sup>2</sup>. This net was the same as that used for sampling *P. octolineatus* concurrently in coastal marine embayments (Veale *et al.* 2015). Both nets were deployed either from the bank and pulled on to the shore or from a boat further from the shore when nearshore waters were particularly shallow, i.e. <0.5 m, and could thus not be effectively sampled by that net. During the present study, the Peel–Harvey Estuary contained numerous conspicuous patches of the macroalgae *Chaetomorpha linum*, *Ulva* spp. and *Cladophora montagneana* and the seagrasses *Halophila ovalis*, *Ruppia megacarpa* and *Zostera* spp. (Valesini *et al.* 2009; Pedretti *et al.* 2011).

*Pelates octolineatus* was also obtained, in March 2009 and January 2011, from the by-catch of a commercial haul net fisher, who was targeting species such as the yellowfin whiting (*Sillago schomburgkii*), the yelloweye mullet (*Aldrichetta forsteri*) and the sea mullet (*Mugil cephalus*) in the area between the inner openings of the Mandurah and Dawesville channels and where water depths were  $\geq 1.5$  m (Fig. 1). The haul net, which was 2 m high, 450 m long and constructed from 51-mm mesh, was deployed in a circle, and then hauled inwards, with the fish then becoming gilled. *Pelates octolineatus* was also obtained opportunistically between December 2009 and March 2010, from the by-catch of a commercial trawl fisher operating at depths of 8 to 13 m in Comet Bay (Jones *et al.* 2010), the large embayment into which the Peel–Harvey Estuary discharges (Fig. 1). The fisher's demersal trawl net, which contained a cod end of 45-mm mesh, was towed three to four times per night for 60 to 80 min at a speed of  $\sim 6.5$  km h<sup>-1</sup>.

### ***Gonadal stages and age***

The total length (TL) and total mass (M) of each *P. octolineatus* were recorded to the nearest 1 mm and 0.01 g. As in the concurrent study of *P. octolineatus* in marine embayments (Veale *et al.* 2015), the gonads of each *P. octolineatus* >100 mm TL, the length at which ovaries and testes typically become distinguishable, were assigned macroscopically to one of the following maturity stages, based on the criteria of Laevastu (1965): I, virgin; II, immature–resting; III, developing; IV, maturing; V–VI, pre-spawning–spawning; VII, spent; VIII, recovering spent. Five ovaries and five testes of *P. octolineatus* at each gonadal stage in each month were subjected to histological examination to confirm that they had been staged correctly. For this purpose, the gonads were placed in Bouin's fixative for 24 to 48 h, depending on their size, and then dehydrated in a series of increasing concentrations of ethanol. The mid-regions of the gonads were embedded in paraffin wax and cut into 6- $\mu$ m transverse sections, then were mounted on microscope slides, stained with either Mallory's trichrome or Ehrlich's haematoxylin and eosin and examined using a compound microscope.

A sagittal otolith from each fish, except for that of the smallest individuals that clearly belonged to the 0+ age class, was sectioned and the number of its opaque zones counted as described in detail for *P. octolineatus* outside the estuary (Veale *et al.* 2015).

### ***Intra- and inter-period comparisons***

The four sites sampled in each of the five regions in the Peel–Harvey Estuary using the 102.5-m seine net in 2008–10 (Fig. 1) included the one or two sites previously sampled in each region with a seine net of the same dimensions on one or two occasions in each season, between summer 1980 and spring 1981 (Loneragan *et al.* 1986) and the three sites sampled in each region in each season, between summer 1996 and spring 1997 (Young and Potter 2003). There are thus seasonal data for the abundance of *P. octolineatus* in the estuary in two consecutive 12 months (i.e. 2 years) in each of 1980–81, 1996–97 and 2008–10. *Pelates octolineatus* was also caught using a 21.5-m seine net in the same months of 1996–97, facilitating comparisons between the relative abundances in that period and 2008–10, recognising; however, that differences between the lengths and mesh sizes in the two nets means that the relative abundances, derived from the samples caught using the two seine nets, cannot be compared directly.

The mean numbers of individuals of the 0+, 1+ and  $\geq 2+$  age classes in samples collected using the 21.5- and 102.5-m seine nets in each calendar season in 2008–10 were calculated and plotted as stacked bar graphs. Note that, because the numbers of fish caught by the 102.5-m seine net in summer and autumn in 2008–10 were very large, the ageing of fish was restricted to large random subsamples (46 and 49% of the total samples respectively), in those two seasons. The proportions of the different age classes displayed in the stacked bar graphs, showing the mean number of fish per sample in each of those seasons, represent those in the large subsamples.

As *P. octolineatus* was not aged in 1980–81, its individuals were assigned either to the 0+ age class or  $\geq 1+$  age classes, which were separated on the basis of whether their lengths were less than or greater than 100 mm TL, the approximate maximum length attained during the first year of life (see Results). Note that the individuals of *P. octolineatus* were neither measured nor aged in 1996–97.

The mean numbers of *P. octolineatus* sampled by the 102.5-m seine net at each site in each calendar season in 1980–81, 1996–97 and 2008–10 were subjected to a two-way analysis of variance (ANOVA) to determine whether the numbers of individuals differed significantly between seasons



(four levels) and periods (three levels), with factors being fixed and the number of replicates in each season in each period being 3 or 4 in 1980–81, 6 in 1996–97, and 7 or 8 in 2008–10. The numbers of fish were shown to require, before analysis, a  $\ln(x + 1)$  transformation to meet the requirements of ANOVA among *a priori* groups (see Clarke and Warwick 2001). When the tests detected a significant difference (i.e.  $P < 0.05$ ), the Scheffé test was employed to ascertain the basis for that difference.

### **Growth**

The growth of the females and males of *P. octolineatus* were each determined by fitting the lengths at age of individuals to the same sine-based seasonal growth model as used for *P. octolineatus* in coastal waters (Veale *et al.* 2015). This model accounts for the seasonality clearly seen in the trends exhibited by modal length classes in sequential monthly samples (see Results). In brief, the model is a modified version of the seasonal growth curve of Somers (1988), which allows for a linear trend in  $k$  with respect to age. The curve may be written as:

$$L_j = L_\infty \left\{ 1 - \exp \left[ - (k_1 + k_2 [t_j - t_0]) \left( t_j - t_0 + \frac{C}{2\pi} [S(t_j) - S(t_0)] \right) \right] \right\}$$

where  $L_j$  and  $t_j$  are the respective length and age of fish  $j$ ,  $L_\infty$  is the asymptotic length,  $t_0$  is the age at which the length of the fish is expected to be zero,  $S(t) = \sin(2\pi(t - t_c))$ ,  $C$  is a constant and  $t_c$  serves as the phase that shifts the sine curve with respect to the age  $t$  and thus determines the period of the year that growth is at a maximum. The value of the von Bertalanffy growth coefficient ( $k$ ) for the  $j$ th fish is  $k_j = k_1 + k_2 (t_j - t_0)$ , where  $k_1$  and  $k_2$  are constants. In this model, the seasonality amplitude parameter ( $C$ ) is constrained to values between 0 and 1.

The growth curve was fitted to the lengths at age for each sex using R (R Core Team 2013) by maximising the log-likelihood, which was calculated under the assumption that deviations of observed from predicted lengths at age were normally distributed with constant variance. Note that the lengths at age of *P. octolineatus* with a TL <100 mm, whose sexes could not be determined from macroscopic examination of gonads, were assigned randomly, but in equal proportions, to the female and male datasets. The hypothesis that a common growth curve could be fitted for the two sexes in the Peel–

Harvey Estuary was rejected at the  $\alpha = 0.05$  level of significance if the likelihood-ratio test (LRT) statistic calculated as twice the difference between the log-likelihoods, obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded  $\chi_{\alpha}^2(q)$ , where  $q$  is the difference between the numbers of parameters in the two approaches. A similar LRT was employed to compare the growth in the estuary with that in coastal waters in the same period (Veale *et al.* 2015). As for *P. octolineatus* in the marine environment (Veale *et al.* 2015), instantaneous rates of change in length were calculated from the fitted sine-based growth curve.

## Results

### *Trends in seasonal water temperatures and salinities*

In 1980–81, the mean seasonal salinities in the five regions of the Peel–Harvey Estuary rose to their maxima in autumn and then declined precipitously to low levels in winter and spring (Fig. 2a). These mean values did differ markedly; however, between regions, particularly in winter when they ranged from ~3 in the Southern Harvey to ~29 in the Mandurah Channel. The highest mean seasonal salinities of 40–44 were recorded in autumn in the Northern and Southern Harvey Estuary and Western Peel Inlet. Although the mean seasonal salinities followed a similar trend in 1996–97, they varied less among regions and, although likewise declining markedly in winter, subsequently recovered more rapidly (Fig. 2b). These differences reflect the influence of the far greater intrusion of sea water during each tidal cycle and its penetration further into the estuary, as a result of the influence of the opening of the large Dawesville Channel in 1994.

Mean seasonal salinities followed similar trends in 2008–10, but were less extreme, typically declining from ~35–40 in summer to ~28 in winter and then rising in spring (Fig. 2c). As in the previous two periods, the maximum mean seasonal salinity was recorded in the Southern Harvey and at a similar level of ~44. The maintenance of higher salinities throughout the estuary in the winter of 2008–10 compared with 1996–97 is because of a reduction in freshwater discharges as a result of declines in rainfall over the last 20 years (Australian Bureau of Meteorology 2014).

The trends exhibited by mean seasonal water temperatures in the five regions were similar in each period, reaching their maxima of 24–27°C in summer and declining to their minima of 13–16°C in winter, before rising sharply in spring (Fig. 2*d, e, f*).

### ***Length and age composition***

Each length class of *Pelates octolineatus* between 0–24 and 175–199 mm TL was represented in samples collected by both the 102.5- and 21.5-m seine nets, but with individuals in length classes comprising the smallest and the largest fish not abundant in catches taken by either net (Fig. 3*a, b*). The data, derived from both seine nets combined, produced modal length classes at 25–50 and 75–100 mm TL respectively, and demonstrated that the samples contained predominantly the 0+ age class (58%) and, to a lesser extent, the 1+ (28%) and 2+ (12%) age classes, and no fish older than 3 years (Fig. 3*c, d*).

The total lengths of *P. octolineatus* in catches taken by commercial haul netting in depths  $\leq 2$  m in summer and early autumn ranged from 108 to 210 mm and, for both sexes, produced a prominent modal length class at 175–199 mm (Fig. 3*e*). Although the far larger mesh size of the haul net than both seine nets explains the far lower numbers of fish with lengths  $>150$  mm in the haul net samples, the upper end of the length range in haul net samples was only slightly greater than in the seine net samples. As fish sampled by the haul net were all  $<4$  years old and most belonged to the 2+ and 3+ age classes (Fig. 3*f*), their maximum age was the same as in the seine net samples (Fig. 3*d*). In the large embayment of Comet Bay, into which the Peel–Harvey Estuary discharges (Fig. 1), the lengths of most *P. octolineatus* caught by commercial trawling in water depths from  $\sim 8$  to 13 m ranged from 125 to 199 mm and produced a modal length class of 150–174 mm (Fig. 3*g*). Most *P.*

*octolineatus* belonged to the 2+ and 3+ age classes, but some were up to 7 years old (Fig. 3*f*).

Whereas females dominated both the length classes of fish  $\geq 175$  mm and the 2+ and 3+ age classes in the haul net samples from the estuary, the reverse trend was exhibited by those obtained by trawling outside the estuary (Figs 3*e–h*).

The new 0+ cohort of *P. octolineatus* was first caught in the Peel–Harvey Estuary in January, when its TL ranged from 17–36 mm and produced a modal length class of 20–29 mm (Fig. 4). By April, the lengths of this age class had increased to between 20 and 49 mm, producing a modal length class of 30–39 mm, which remained until July–August and then increased to 80–89 mm in November (Fig. 4). The corresponding cohort, now 1+, increased in length between December and March. The 1+ age class was not caught between May and August, but did appear again in small numbers from September to November. Appreciable numbers of the corresponding cohort, now 2+, were caught in December and, together with a very small number of 3+ fish, were present until March, after which they were no longer caught (Fig. 4).

### ***Seasonal and inter-decadal comparisons in relative abundances***

The *P. octolineatus* caught by both the 102.5- and 21.5-m seine nets in summer in 2008–10 comprised mainly 1+ and older fish, the latter very largely comprising 2+ fish (Fig. 5a, b). These age classes declined markedly in abundance in the samples collected by both nets in autumn and were absent in those from winter and present in only very low numbers in those from spring. The 0+ age class was at least relatively abundant in the samples collected by both nets in each season and particularly spring. The trends exhibited by the proportions of young and old fish in sequential seasonal samples in 1980–81 were similar to 2008–10, in that  $\geq 1+$  fish dominated summer samples and 0+ fish dominated spring samples (Fig. 5c). The very large numbers of 0+ fish caught in winter 1980–81 were because of two exceptionally large catches when the net also collected an unusually large amount of macroalgae. Two-way ANOVA demonstrated that the mean number of *P. octolineatus* in samples obtained using the 102.5-m seine net in each season in 1980–81, 1996–97 and 2008–10 differed significantly among those periods and seasons and that the interaction between these main effects was not significant (Table 1). The mean number of *P. octolineatus* was significantly less in 1996–97 compared with both 1980–81 ( $P = 0.002$ ) and 2008–10 ( $P = 0.003$ ), which were not significantly different ( $P = 0.697$ ). This difference reflects the fact that, in each season, the mean number of fish per sample in 1996–97 was lower than in both 1980–81 and 2008–10 (Fig. 6). In terms of season, the mean number of *P. octolineatus* per sample was significantly greater in summer than winter ( $P = 0.002$ ).

### ***Growth***

As the growth curves of female and male *P. octolineatus* in the Peel–Harvey Estuary did not differ significantly ( $P > 0.05$ ), a sine-curve based seasonal growth model was fitted to the lengths at age of both sexes combined (Fig. 7; Table 2). Note that there are no data for the lengths at age of older fish in winter as such fish were not caught in the estuary in that season, having presumably left this system (see Fig. 4 and Discussion). The growth curve of *P. octolineatus* in the estuary differed significantly ( $P < 0.001$ ) from that derived for this species in the marine environment. The instantaneous daily growth rates of *P. octolineatus* peaked in summer and declined to a minimum in winter (Fig. 8). Growth peaked slightly earlier and at a greater level in the estuary than in coastal waters.

### ***Gonadal development***

The gonads of the majority of the 93 fish caught in the Mandurah Channel from November to January, when this species spawns in coastal marine waters (Veale *et al.* 2015), were either at stages V–VI (33%) or VII (53%). The 76 large *P. octolineatus* caught in January by haul netting in Western Peel Inlet, and thus near the two entrance channels, possessed gonads predominantly at stages IV and V–VI (84%). However, as no ovary at stage V–VI contained macroscopically visible hydrated oocytes, and no testis at stage V–VI readily produced milt when external pressure was applied to the body, these gonads were presumably at stage V (pre-spawning) rather than stage VI (spawning). Furthermore, no large fish possessing gonads at stages VII or VIII (i.e. spent or recovering spent) was caught in the estuary. In contrast, 36% of the 103 *P. octolineatus*, caught between December and February by trawling in Comet Bay outside the estuary, contained gonads that were clearly identifiable macroscopically as possessing hydrated oocytes or readily released milt and a further 10% were spent.

## Discussion

### *Evidence that the Peel–Harvey Estuary is a nursery area for *Pelates octolineatus**

Any attempt to determine whether an area provides a nursery function for a species needs to demonstrate that large numbers of juveniles of that species are found in the area and that this area is separate from the areas in the vicinity where spawning occurs (Beck *et al.* 2001). It is clear from the results of the present study that the juveniles of *Pelates octolineatus* are highly abundant in the Peel–Harvey Estuary, and particularly when the biomass of macrophytes is substantial. In a concomitant study, *P. octolineatus* was shown to spawn from late spring (November) to mid-summer (January) in coastal marine embayments further north, on the lower-west coast of Australia (Veale *et al.* 2015). During that period, the gonads of most (98%) of the 796 individuals caught by sampling in the basins of the Peel–Harvey Estuary were either immature–resting (stage I–II) or developing–maturing (stage III–IV), with only 1% at stages V–VI (mature–spawning), VII (spent) or VIII (recovering spent) and none was running ripe. This clearly implies that the *P. octolineatus* found in the large main body of the estuary spawn in the marine environment. The collection of some *P. octolineatus* with gonads at stages V–VI and VII in the Mandurah entrance channel suggests that a few individuals may spawn in this short stretch of water (Veale *et al.* 2015), in which salinity is the same as seawater (35) during the spawning period of *P. octolineatus*.

The presence of a few *P. octolineatus* with TLs of 17–20 mm in the January samples from the Peel–Harvey Estuary demonstrates that this species starts recruiting into the estuary at lengths at or slightly above the 11 mm at which this terapontid metamorphoses (Neira *et al.* 1998). As these individuals were caught in Peel Inlet, and not far from the inner opening of the Mandurah entrance channel (Fig. 1), they had presumably been spawned just outside the estuary and possibly also in the channel (see above). As the TLs of most females and males of *P. octolineatus* were less than 141 and 131 mm, the lengths at which 50% of each of those sexes reached maturity (TL<sub>50</sub>) in the marine environment (Veale *et al.* 2015), this terapontid uses the Peel–Harvey Estuary predominantly during juvenile life. This parallels the situation with *Pelates sexlineatus* on the east coast of Australia, where this

congeneric terapontid enters estuaries in large numbers, but typically spawns in coastal marine waters immediately outside those systems (Smith and Suthers 2000).

### ***Length and age compositions***

It is noteworthy that each 25-mm length class of *P. octolineatus* up to 175–199 mm was represented in the large samples obtained from the Peel–Harvey Estuary by two seine nets of different sizes. Furthermore, the length class of 175–199 mm is only slightly less than 200–224 mm, which constituted the upper end of the length range in samples taken by the 51 mm mesh of the haul net of the commercial fisher, who targets large individuals of certain species in the Peel–Harvey Estuary. As the haul net samples were collected in January and March, they were obtained during the period when the largest *P. octolineatus* occupy the estuary (see below). It is thus concluded that the samples obtained by both methods collectively represent the length range of *P. octolineatus* present in the Peel–Harvey Estuary. Moreover, the oldest *P. octolineatus* caught in the Peel–Harvey Estuary by both seine and haul netting belonged to the 3+ age class and thus all of the numerous individuals of this species that were aged were less than 4 years old.

The progression exhibited by the modal length classes of aged fish in sequential monthly length–frequency distributions demonstrates that, in the Peel–Harvey Estuary, *P. octolineatus* is represented by the 0+ age class continuously from January to November and then, as it becomes 1-year-old, by substantial numbers of 1+ fish until March and by a few 1+ fish in April. As the lengths of all 0+ fish in January lay between 17 and 33 mm, and those of most 1+ fish in April ranged from 122–155 mm, the trends shown by the monthly length distributions also emphasise that *P. octolineatus* undergoes considerable growth during its first 15–16 months in the Peel–Harvey Estuary. Those trends also emphasise; however, that most growth occurs between September, i.e. early spring, and March, i.e. early autumn (see below). Although fish  $\geq 2+$  in age were not as abundant as those of the 1+ age class, they were still likewise confined mainly to the months between December and March.

### ***Emigration from the estuary***

As previously concluded, the juveniles of *P. octolineatus* in 2008–10 first entered the Peel–Harvey Estuary in summer and many remained there until early autumn (March) of the following year, i.e. 15 months later, and several 2+ and a few 3+ fish entered the estuary in summer and, as with 1+ fish, also left the estuary in early autumn. This trend in movements parallels that exhibited by *P. octolineatus* in 1980–81, where, in contrast to the situation in December and March of 2008–10, the lengths of none of the ~1500 individuals caught in June and August exceeded 120 mm, and most were <100 mm (Potter *et al.* 1983) and would thus have represented the 0+ age class. The fact that many 0+ *P. octolineatus* remained in the estuary during winter, whereas the 1+, 2+ and 3+ age classes had left by that season, is presumably related to the timing and location of spawning. It is particularly relevant therefore that, whereas very few fish reach maturity at the end of their first year of life, virtually all older fish become mature at the end of the second and subsequent years of life, and typically spawn in marine waters outside the estuary (Veale *et al.* 2015). Although it would probably be advantageous for younger fish to remain in the productive and protected environment of the main body of the estuary, there would be selection pressures, at some time, for the older fish to emigrate from the estuary in preparation for spawning. Thus, older *P. octolineatus* presumably become receptive to environmental cue(s) that trigger emigration in autumn and thus before late winter, when daylength and water temperatures start to increase and gonadal recrudescence is initiated in the marine environment (Veale *et al.* 2015). The greater numbers of females than males in the 2+ and 3+ age classes in the haul net samples obtained from the estuary during the spawning period suggests that females show a greater tendency to return to the estuary after they have reached maturity. This conclusion is consistent with females predominating in the corresponding age classes in the seine net samples from the estuary and for males to predominate in those age classes in the trawl samples from Comet Bay outside the estuary.

The abundance of older fish declined when freshwater discharge increased from negligible volumes in summer (Australian Bureau of Meteorology 2014) and thus produced a concomitant decline in salinity which occurred in tandem with temperature (Fig. 2). Thus, as these variables were correlated, it is



difficult to tease out whether any one of them played an overriding role in stimulating emigration. The greater tolerance of juveniles of marine estuarine-opportunists to low salinities (Holliday 1971; Bell *et al.* 1984) would help account; however, for many juveniles remaining in the Peel–Harvey Estuary during winter. Yet, the observation that the majority of *P. octolineatus*, which included predominantly 0+ individuals, left the main body of the Blackwood River Estuary to the south of the Peel–Harvey Estuary during a period of extreme freshwater discharge, suggests that, under such circumstances, flushing can play a major role in driving this species out of estuaries (Valesini *et al.* 1997).

### ***Habitat and inter-decadal comparisons of abundance***

As *P. octolineatus* was found predominantly in and around macroalgae in 1980–81 and macroalgae and seagrass in 2008–10, the macrophytes within the Peel–Harvey Estuary are considered a crucial habitat for this species. As dense seagrass is not present in nearshore marine waters immediately to the north or south of the Peel–Harvey Estuary, the macrophytes in this estuary presumably constitute the main nursery habitat for the progeny of the adults that spawn in nearby marine waters. This conclusion would be consistent with the results of an earlier study, which demonstrated that, in nearshore waters along the lower west coast of Australia, *P. octolineatus* was regularly abundant only in areas of dense seagrass (Valesini *et al.* 2004).

In contrast to the situation in nearshore waters along the coast in the region of the Peel–Harvey Estuary, the protected environment of Mangles Bay to the north (Fig. 1) possesses extensive and dense seagrass beds, which contain large numbers of 0+ *P. octolineatus* (Valesini *et al.* 2004; Veale *et al.* 2015). It is therefore proposed that, when dense seagrass beds are available in the marine environment near its spawning areas, *P. octolineatus* uses the beds as a nursery area and completes its life cycle in the marine environment. Where there is, however, a paucity of such macrophytes, this marine-estuarine opportunist species uses the macrophyte beds in estuaries as an alternative nursery area.

The importance of plant material as a habitat for *P. octolineatus* is further emphasised by this terapontid being more abundant than any other fish species caught by Burkholder *et al.* (2013) in

seagrass meadows in a large sub-tropical embayment well to the north of the Peel–Harvey Estuary. Plant material provides protection and a major food source for *P. octolineatus* to such an extent in the sub-tropical embayment, that its grazing may have a significant effect on the seagrass biomass in that environment (Burkholder *et al.* 2013). There can be little doubt that the success of *P. octolineatus* depends on the presence of substantial macrophyte growths and thus this terapontid differs from the majority of commercially important fish and invertebrate species on the north-eastern seaboard of the United States of America, which use seagrass meadows but can survive well in unvegetated areas (Heck *et al.* 1995; Able and Fahay 1998).

Our analyses show that *P. octolineatus* was more abundant in the Peel–Harvey Estuary in 1980–81, when massive growths of macroalgae were present, than in 1996–97 when macroalgal biomass had declined through increased flushing of the system, and to the abundance of this terapontid subsequently rising when the biomass of macrophytes increased. These inter-period differences in relative abundance are reflected in *P. octolineatus* contributing as much as 37 and 2.5% to the total number of fishes caught in this estuary by the 102.5-m seine net in 1980–81 and 2008–10 respectively, compared with only 0.1% in 1996–97. Indeed, *P. octolineatus* was so numerous in 1980–81 that its abundance was the greatest of any fish species during that period of extreme macroalgal growth.

### **Growth**

The pattern of residuals from the sine-based seasonal growth model fitted to the lengths at age (Fig. 7) confirmed that growth of *P. octolineatus* in the Peel–Harvey Estuary is conspicuously seasonal, thus paralleling the situation in nearby coastal marine waters of south-western Australia (Veale *et al.* 2015). Although the instantaneous daily growth rate of *P. octolineatus* during the first 15–16 months of life produced a sharp peak, as it also does in coastal marine waters (Veale *et al.* 2015), the peak occurred slightly earlier, i.e. early- v. late-summer. It is therefore relevant that water temperatures peaked earlier in the estuary than in nearby coastal marine waters (Fig. 8a). Furthermore, the maximum instantaneous growth rate of *P. octolineatus* of  $0.42 \text{ mm day}^{-1}$  in the Peel–Harvey Estuary was greater than the  $0.35 \text{ mm day}^{-1}$  recorded for this species in marine

embayments on the same coast. The faster growth of the juveniles of this marine estuarine-opportunist species in the estuarine environment, compared to those in the marine environment, parallels the situation with the juveniles of *Solea solea* in France and *Platichthyes bicoloratus* in Japan (Le Pape *et al.* 2003; Yamashita *et al.* 2003). It contrasts, however, with the situation with five species on the temperate east coast of North America where growth was not found to differ between estuaries and the inner continental shelf (Woodland *et al.* 2012).

### **Summary**

In summary, the results of the present study, when considered in conjunction with those of previous and concurrent studies (Potter *et al.* 1983; Young and Potter 2003; Veale *et al.* 2015), provide important insights as to how marine estuarine-opportunists, such as *P. octolineatus*, use alternative nursery environments. As the estuarine environment is typically more productive than coastal marine waters, such differences could account for the growth of juveniles of *P. octolineatus* in the Peel–Harvey Estuary being faster than those that remained in their natal marine environment. A rapid attainment of a substantial size would make individuals less susceptible to predation (Blaber and Blaber 1980; Kennish 1990; Yamashita *et al.* 2003; Potter *et al.* 2015). Although estuaries can also suffer from potentially deleterious anthropogenic effects, such as those caused by nutrient enrichment runoff from surrounding land, which has been cleared for agricultural and other purposes, the resulting growth of macrophytes can be beneficial to certain species. The juveniles of the macrophyte-associated *P. octolineatus* have demonstrably been a beneficiary in the eutrophic Peel–Harvey Estuary, with macroalgae, and also more recently by seagrass and macroalgae, providing abundant cover and an even richer food source than is usual in estuaries. The results also provide overwhelming circumstantial evidence that some juveniles of *P. octolineatus* capitalise on the benefits of this microtidal estuary by remaining there for over 1 year, before emigrating and spawning at the completion of their second year of life.

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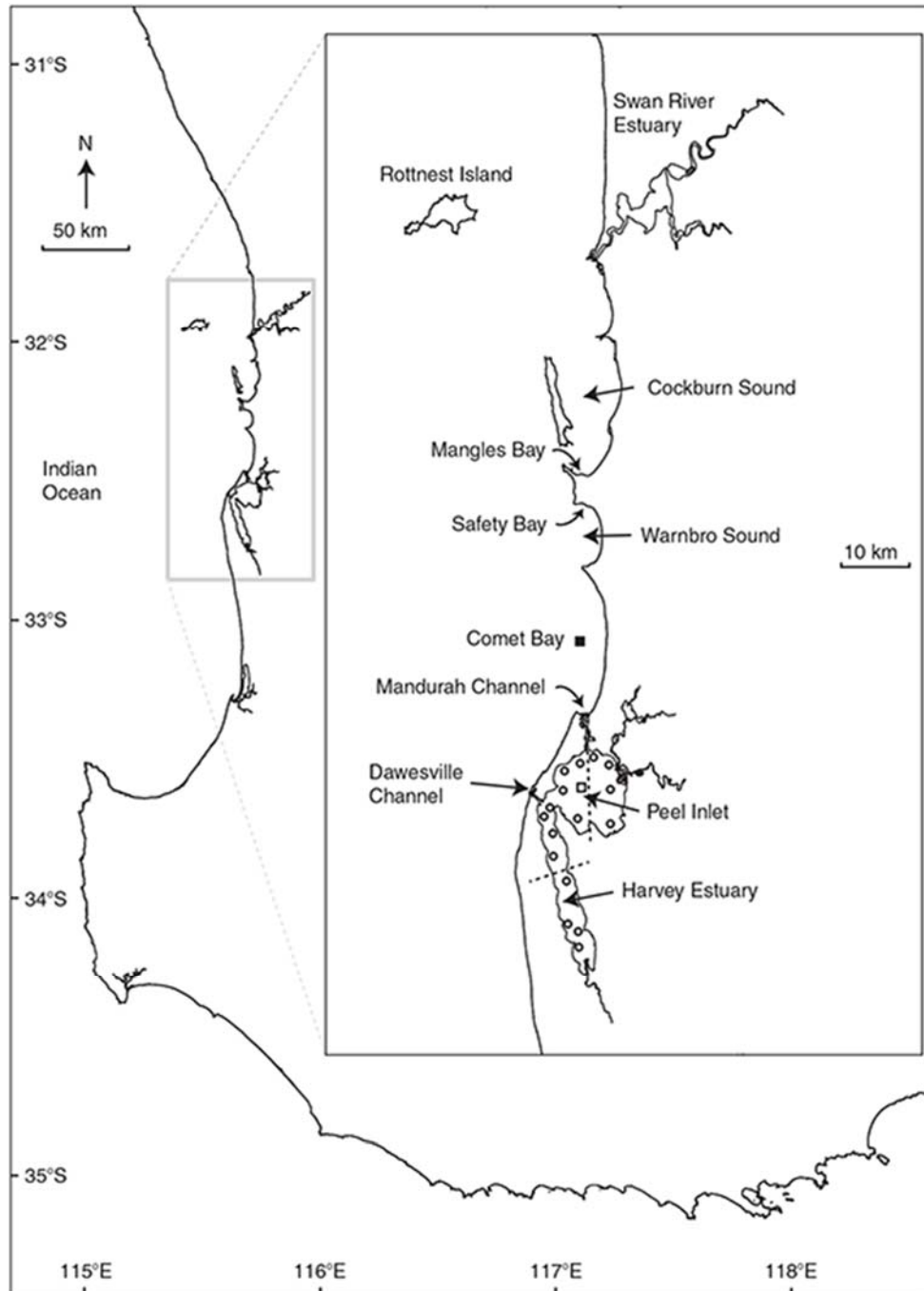
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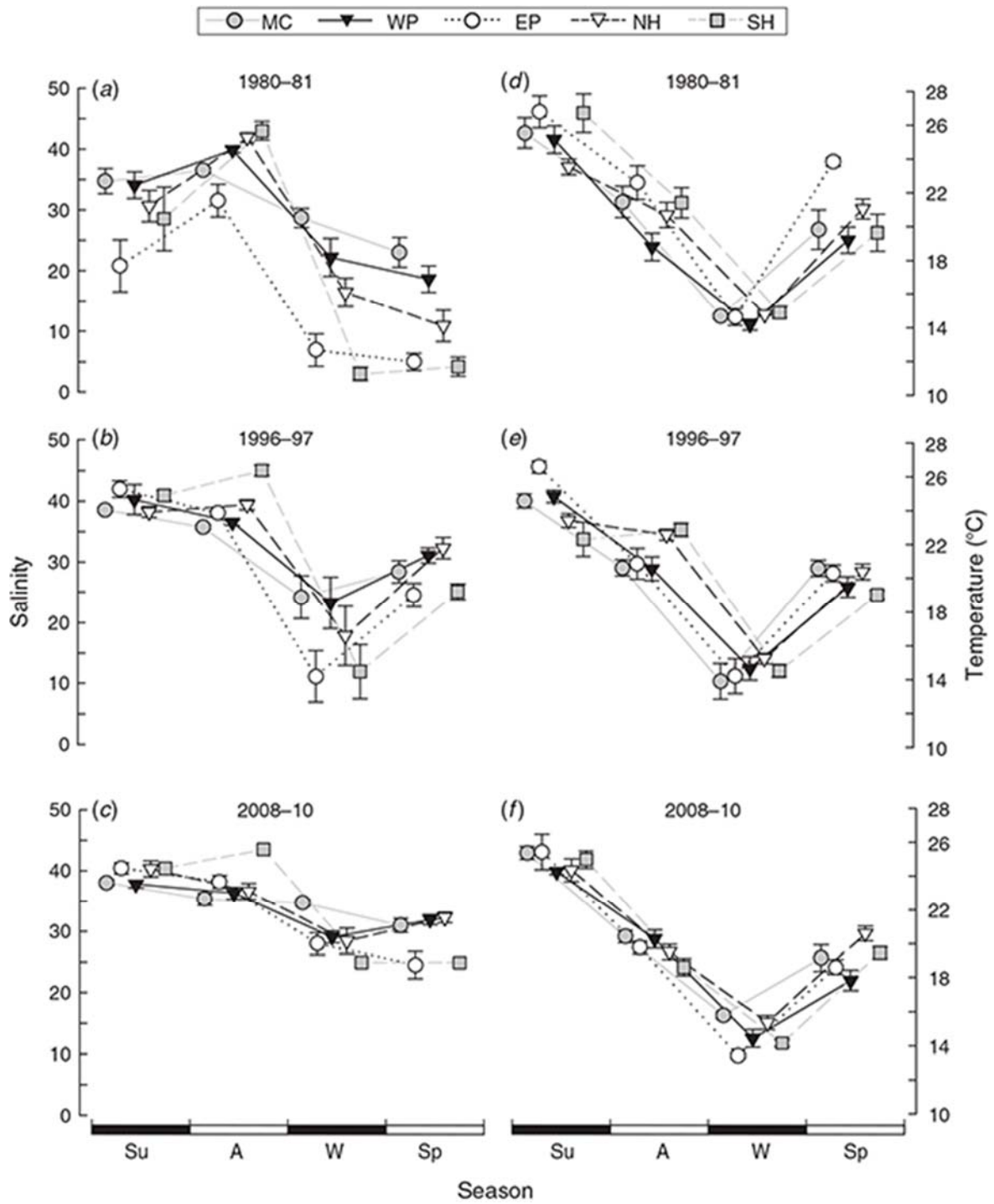
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**Fig. 1.** Map of south-western Australian coast showing the region (vertical rectangular box) in which *Pelates octolineatus* was sampled seasonally between winter 2008 and autumn 2010. Inset shows sampling locations in the Peel–Harvey Estuary and Comet Bay, including seine net sites (open circles), a commercial haul netting site (open square) and a commercial trawling site (closed square). Inset also shows the locations of Mangles Bay and Safety Bay sampled in a concurrent study (Veale *et al.* 2015). Dashed lines divide the Western and Eastern Peel Inlet regions and Northern and Southern Harvey Estuary regions.

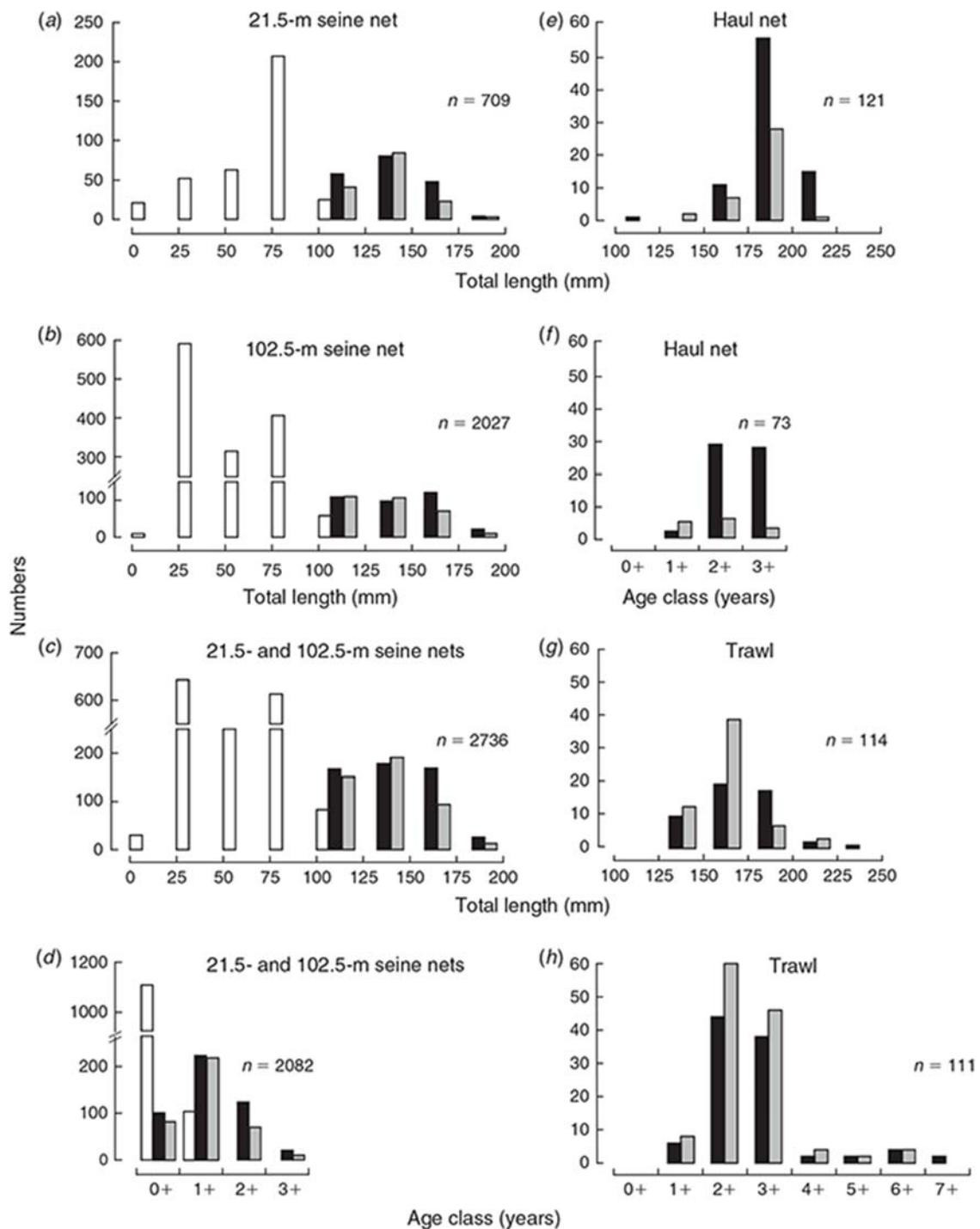




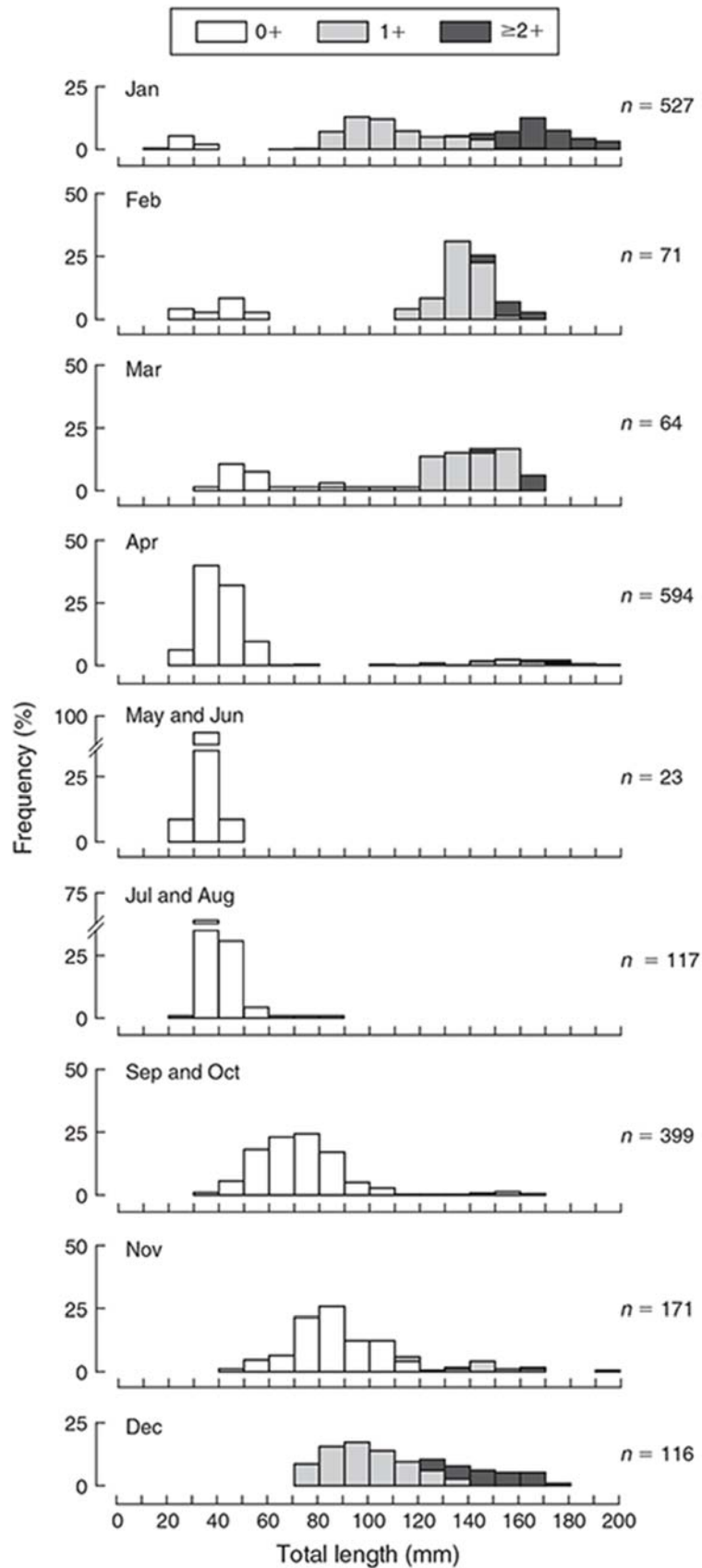
**Fig. 2.** Mean seasonal salinities and water temperatures  $\pm 1$  s.e. in the five regions sampled in the Peel–Harvey Estuary, i.e. Mandurah Channel (MC), Western Peel (WP), Eastern Peel (EP), Northern Harvey (NH) and Southern Harvey (SH), in the summer (Su), autumn (A), winter (W) and spring (Sp) of 1980–81, 1996–97 and 2008–10.



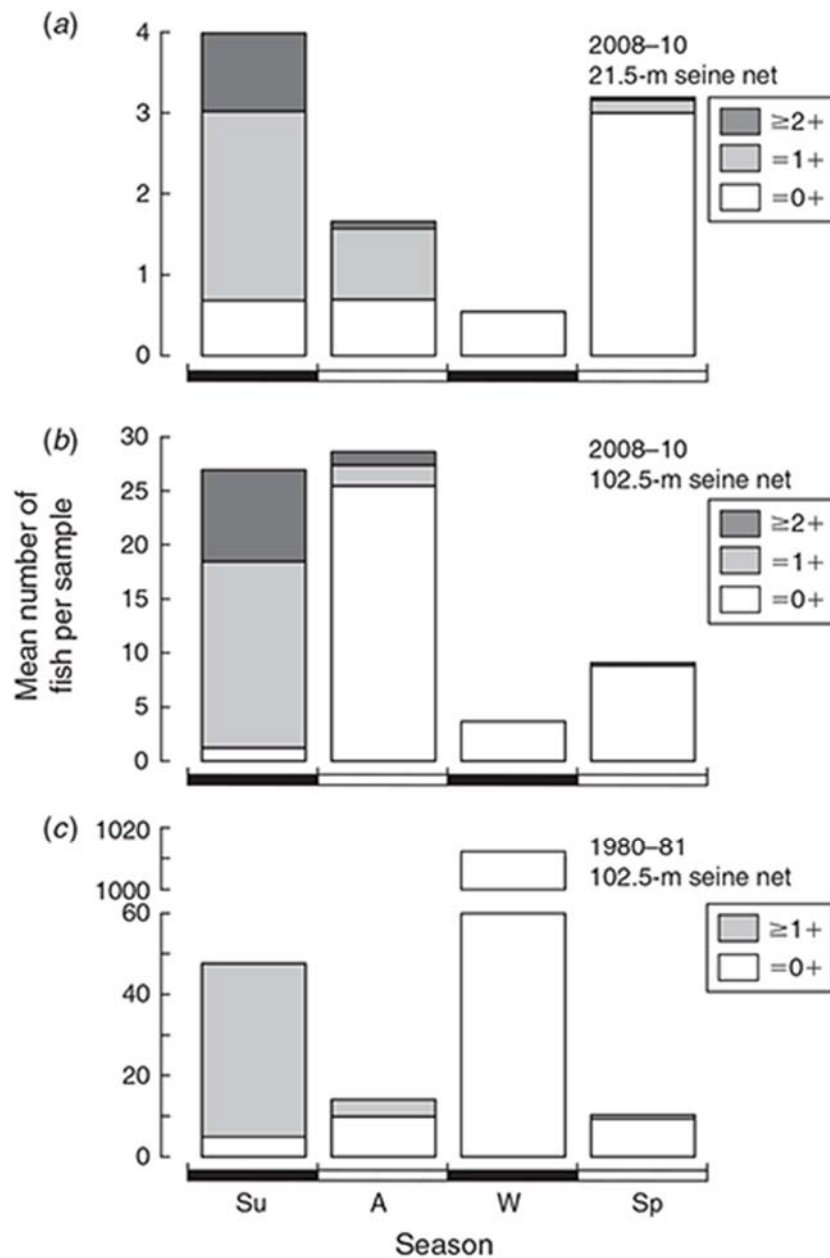
**Fig. 3.** Length and age-frequency distributions for unsexed individuals (white histograms), females (black histograms) and males (grey histograms) of *Pelates octolineatus* caught in the Peel–Harvey Estuary by (a–d) seine netting, (e, f) commercial haul netting and (g, h) commercial trawling in Comet Bay outside the estuary. N.B. Data from both seine nets are combined in c and d. Seine netting was undertaken at least once seasonally between winter 2008 and autumn 2010, haul netting in January 2009 and March 2010 and trawling between December 2009 and March 2010. *n*, sample size.



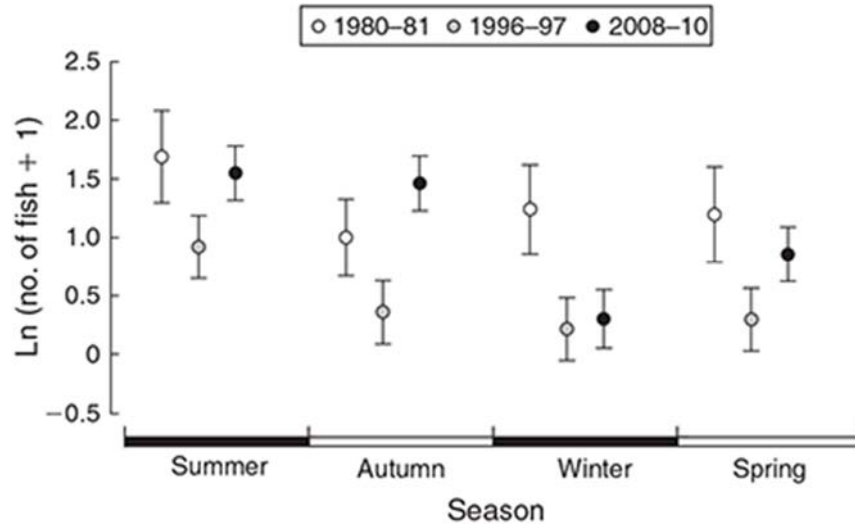
**Fig. 4.** Monthly length–frequency distributions for the different age classes of *Pelates octolineatus* caught by the 21.5- and 102.5-m seine nets in the Peel–Harvey Estuary between winter 2008 and autumn 2010. *n*, sample size.



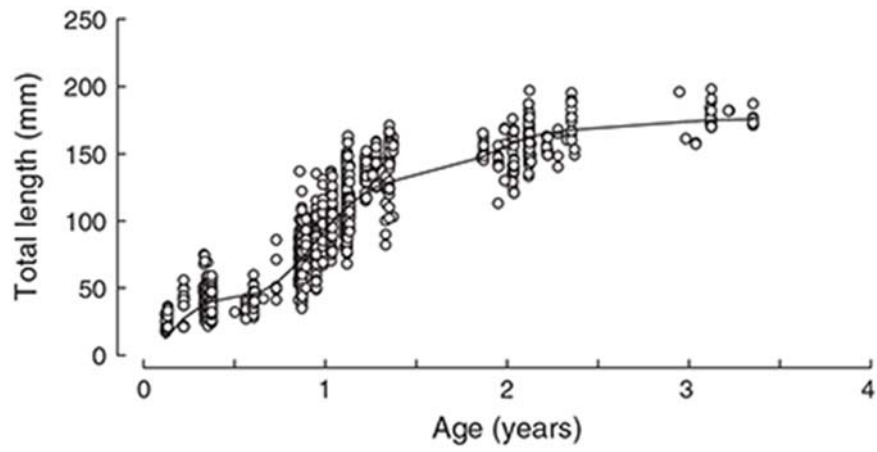
**Fig. 5.** Bar graphs showing the mean number of *Pelates octolineatus* caught per sample in the Peel–Harvey Estuary using (a) 21.5- and (b) 102.5-m seine nets in each calendar season between winter 2008 and autumn 2010 and (c) using a 102.5-m seine net in each calendar season in 1980–81. The mean numbers of the 0+, 1+ and  $\geq 2+$  age classes are shown in (a) and (b) and the mean numbers of fish assigned to the 0+ and  $\geq 1+$  age classes on the basis of their lengths are shown in (c). The sequence in this Fig. and Fig. 7 commences in summer when the first 0+ fish are caught.



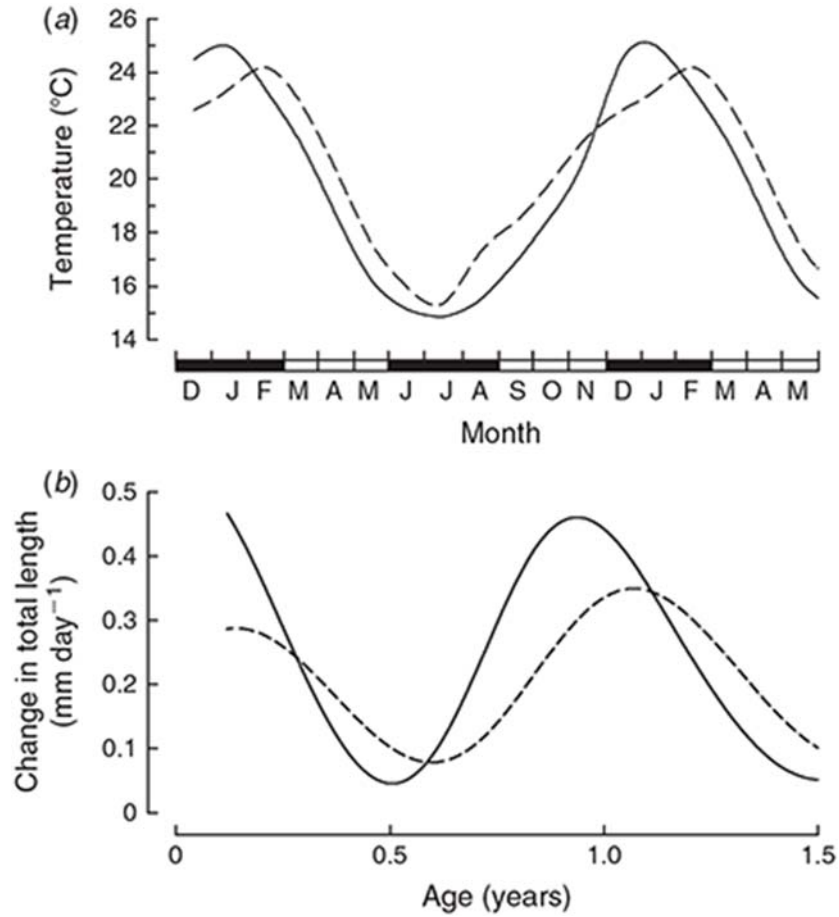
**Fig. 6.** Mean  $\pm 1$  s.e. of  $\ln(x + 1)$  transformed number of *Pelates octolineatus* in each sample from the Peel–Harvey Estuary in each calendar season using the 102.5-m seine net in 1980–1981, 1996–1997 and 2008–2010.



**Fig. 7.** Sine curve-based seasonal growth model fitted to the lengths at age of *Pelates octolineatus* caught in the Peel–Harvey Estuary in 2008–2010.



**Fig. 8.** Trends exhibited by (a) monthly temperatures in the Peel–Harvey Estuary (solid line) and marine embayments (dashed line) over 18 months derived using a loess smoothing function and (b) instantaneous growth rates of *Pelates octolineatus* in the Peel–Harvey Estuary (solid line) and marine embayments (dashed line) derived from the sine-curve based growth model.



**Table 1. Mean squares (MS) and significance levels (*P*) for two-way ANOVA of the numbers of *Pelates octolineatus* caught per sample in the Peel–Harvey Estuary in each calendar season over 2 years in 1980–81, 1995–1996 and 2008–2010**

d.f., degrees of freedom; *F*, *F* statistic

	d.f.	MS	<i>F</i>	<i>P</i>
Period	2	18.199	8.41	0.001
Season	3	8.058	3.724	0.012
Period × Season	6	2.525	1.167	0.324
Residual	325	2.164		



**Table 2. Parameters and 95% confidence intervals (CI) for the sine-curve based seasonal growth model fitted to the lengths at ages of *Pelates octolineatus***

$L_{\infty}$  is the asymptotic total length (mm),  $k_1$  and  $k_2$  are the coefficients of the linear relationship of the growth coefficient ( $\text{year}^{-1}$ ),  $k$ , with age,  $t_0$  is the hypothetical age (years) at which fish would have zero length, and  $C$  and  $t_c$  relate to the seasonality in growth

Parameter	Estimate	95% CI
$L_{\infty}$	177	174–179
$k_1$	0.55	0.51–0.60
$k_2$	0.30	0.28–0.33
$t_0$	0.05	0.04–0.07
$C$	1.00	1.00–1.00
$t_c$	0.005	0.00–0.02