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Age and size compositions, habitats, growth and reproductive characteristics of a terapontid (*Pelates octolineatus*) in coastal waters

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Abstract

This study of *Pelates octolineatus* is the first to use individually aged fish to describe the life cycle of a terapontid, a speciose and abundant Indo-West Pacific family. On the lower west Australian coast, this species uses dense seagrass as a nursery area and, after ~1 year of life when approaching 100 mm in total length (TL), moves into deeper waters over sparser seagrass where it matures at the end of its second year at ~140–170 mm. The maximum TL and age were 256 mm and 10 years. A modified von Bertalanffy curve, allowing for a linear increase in the growth coefficient with age, improved the fit to the lengths at age of older *P. octolineatus*. Growth was even better described by extending this model to allow for seasonality through incorporating a sine-based curve. This model described well the seasonality exhibited by modal progressions in monthly length–frequency distributions. Instantaneous growth rates, particularly of the youngest age classes, peaked in the warm, summer months and the

amplitude of seasonal change in these rates declined with increasing age. Gonadal recrudescence occurred in early spring as temperature and day length increased and spawning peaked in late-spring to mid-summer when temperatures were approaching their maxima.

Additional keywords: Grunters, movements, seagrass, sine curve-based seasonal growth model, south-western Australia.

Introduction

Numerous fish species spawn in coastal waters and use, as a nursery area, the sheltered habitats found in inshore waters such as seagrass, surf zones, rocky shores, mangroves and unvegetated soft substrata (Bennett 1989; Harmelin-Vivien *et al.* 1995; Valesini *et al.* 2004), with some of these species also employing those in estuaries for this purpose (Blaber and Blaber 1980; Vasconcelos *et al.* 2008; Woodland *et al.* 2012; Potter *et al.* 2013). Following the completion of their juvenile phase, many of these marine species move into deeper coastal waters, to different habitats, or to both, where they mature and spawn (e.g. Blaber 2000; Hesp *et al.* 2004; Able 2005).

The growth of many fish species is seasonal, occurring more rapidly in the warm summer than cool winter months (Pitcher and Macdonald 1973). Although descriptions of the growth of most marine species have not employed a model structure that takes such seasonality into account, seasonal models have been shown, in certain cases, to provide a better fit to the lengths at age than those derived using a traditional von Bertalanffy growth curve (e.g. McGarvey and Fowler 2002; Porch *et al.* 2002; Garcia-Berthou *et al.* 2012).

The Terapontidae (Grunters or Tigerperches) contains ~48 fish species representing 16 genera, including the genus *Pelates* (Nelson 2006). This family is widely distributed in the marine coastal, brackish and freshwaters of the Indo-West Pacific from Africa to Japan, Fiji and Samoa, with at least 22 of these species occurring in Australian waters, where some are particularly abundant (Morgan *et al.* 1998; Davis *et al.* 2011). Seagrass provides a nursery habitat for the eastern striped grunter *Pelates*

sexlineatus in estuaries in eastern Australia (Smith and Suthers 2000) and for its congener the western striped grunter *Pelates octolineatus* and the sea trumpeter *Pelsartia humeralis* in coastal marine waters in south-western Australia (Valesini *et al.* 1997, 2004; Crawley *et al.* 2006; Wakefield *et al.* 2013).

The young juveniles of *P. sexlineatus* settle in shallow, fine-scale seagrass beds, and especially of *Zostera capricorni* (Smith and Suthers 2000), and then, as they increase in age and size, move out into deeper waters over larger seagrass, i.e. *Posidonia australis* (K. Smith, pers. comm.). Because *P. octolineatus* is the most abundant of all teleosts in the seagrass meadows of Shark Bay on the west coast of Australia, and consumes the entire widths of seagrass blades, this terapontid could have a marked effect on the biomass of this seagrass and thus play a major role in the structure and function of that macrophyte habitat in at least this large sub-tropical embayment (Burkholder *et al.* 2012).

Although the catches of *P. octolineatus* were low in fish samples collected along the lower west coast of Australia during extensive trawling in water depths of 5–15 m and 1–4 km from the shore, they did contain large individuals (Hyndes *et al.* 1999), indicating that *P. octolineatus* migrates further from the shore and into deeper waters as it increases in size and age. The larger individuals of this terapontid make small contributions to the commercial and recreational catches in South Australia (Fowler *et al.* 2008) and, although sold very occasionally in fish markets in Western Australia, are not targeted by recreational fishers in that state.

Although terapontid species are abundant in various regions and occupy a range of environments, detailed composite studies of the age composition, growth and reproductive biology of the species in this family have been undertaken only in the case of the yellowtail grunter *Amniataba caudavittata* in a south-western Australian estuary (Potter *et al.* 1994; Wise *et al.* 1994). In that study, however, the growth zones in whole otoliths could only be used to age fish up to 18–22 months old, which meant that age compositions and growth had to be determined by analysing modal progressions in length–frequency distributions (Wise *et al.* 1994). Those data still clearly revealed, however, that the growth of this essentially sub-tropical terapontid was seasonal in this temperate estuary and was greatest in the warmer months of the year. There were also indications from length–frequency data that those

individuals of *P. octolineatus* that enter estuaries exhibit seasonal growth in these systems and that spawning occurs during spring and summer in coastal marine waters (Potter *et al.* 1983).

Samples of *P. octolineatus* were obtained from nearshore, shallow (≤ 2 m) and deeper, more offshore (~2–15 m) waters in coastal marine embayments on the lower west coast of Australia. The resultant data were used to determine the size and age compositions, habitats, growth and reproductive characteristics of this terapontid. The analyses were aimed initially at testing the hypothesis that, with increasing age and size, *P. octolineatus* moves from its nursery areas in dense seagrass meadows into deeper waters where it matures and spawns. Emphasis was placed on determining the sizes and ages when such movements occur and at which maturity is attained. The hypotheses were tested that, like many temperate species that spawn in summer (Lam 1983), gonadal recrudescence is associated with increasing water temperature and day length and that spawning is initiated when water temperatures are rising. The lengths at age of *P. octolineatus* were used to test whether a seasonal growth model yielded a better fit to the lengths at age than that produced by a traditional von Bertalanffy growth curve.

Materials and methods

Sampling regime and analyses of abundances

Pelates octolineatus was sampled by seine netting throughout the dense seagrass meadows (mainly *Posidonia sinuosa*) in the nearshore, shallow (<1.5 m) and sheltered waters of Mangles Bay at the southern end of the large marine embayment of Cockburn Sound, on the lower west coast of Australia (Fig. 1). The seine net, which was 21.5 m long and 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, covered an area of 116 m². The net was laid parallel to the shore and the ends of its wings pulled inwards to form a semi-circle within the seagrass and then dragged onto the beach. Note that nearshore sampling focussed on Mangles Bay, because its nearshore waters were known to contain substantial areas of dense seagrass, which constitute the dominant habitat of this terapontid (Valesini *et al.* 2004; Wakefield *et al.* 2013). *Pelates*

octolineatus was also sampled throughout seagrass (mainly *P. sinuosa*) in the immediately adjacent offshore, deeper (~2–8 m) waters of Mangles Bay and in corresponding patchy seagrass beds at similar water depths of Safety Bay in the northern region of Warnbro Sound (Fig. 1). These waters were sampled from a boat by rod and line, using small (size 12) long-shank hooks and employing squid (*Sepioteuthis australis*) and prawns (*Kishinouyepenaeopsis cornuta*) as bait. Note that sampling of the waters in both Mangles Bay and Safety Bay covered regions that stretched ~1 km along the coastlines of those bays.

The nearshore and offshore waters in Mangles Bay and the offshore waters in Safety Bay were sampled monthly from March 2009 to February 2011 and from June 2009 to February 2011 respectively. In each month, seine netting was undertaken at three nearshore sites, ~50 m apart, in Mangles Bay, and rod and line fishing was conducted over an area of ~1–2 km² for 4–6 h at a distance of 200–500 m from the shore. On each sampling occasion, the salinity and water temperature at each site were measured in the middle of the water column using a Yellow Springs International Model 85. The durations of daylight in the sampling area during this study were obtained from the website www.timeanddate.com.

The numbers of *P. octolineatus* sampled at each site in Mangles Bay using the 21.5-m net in each corresponding season of the year were subjected to one-way ANOVA to determine whether the relative abundances of this species in these nearshore waters change significantly during the year. The numbers of *P. octolineatus* were shown, by a plot of the natural logarithms of the means and standard deviations of the data for each season, to require a $1/(x + 1)$ transformation to meet the test assumption of homogeneous dispersions among *a priori* groups (Clarke and Warwick 2001). Levene's test demonstrated that this transformation stabilised the variances.

Age determination

The total mass (M) and total length (TL) of each *P. octolineatus* were recorded to the nearest 0.01 g and 1 mm. The sagittal otoliths were removed from all *P. octolineatus* caught in the marine bays in each month, except when, with seine netting, a sample exceeded 100 fish, in which case the otoliths

were removed from a random subsample of 25–50% of those fish for analyses. One of the sagittal otoliths from each fish was cleaned, embedded in clear epoxy resin, and cut transversely through the primordium into ~0.3-mm sections employing a Buehler IsoMet low speed saw and mounted on microscope slides under glass coverslips using DePX mounting adhesive. Each otolith section was examined against a black background employing a Leica Mz7.5 dissecting microscope and reflected light. A digital image of each otolith section was recorded with a Leica DC300 camera and analysed using the computer imaging package Leica Application Suite (*ver.*3.0), which enabled the opaque zones to be readily identified and counted. Because the otoliths of *P. octolineatus* are fragile, the selected otolith was sometimes damaged on removal or during sectioning and thus the other otolith from that fish was then sectioned. For ~10% of fish, both otoliths were damaged or did not possess clearly defined opaque zones and could not therefore be used for ageing.

The opaque zones in each sectioned otolith were counted twice by the first author and on a third occasion when those counts were not the same. In the latter cases, which occurred with only ~5% of the otoliths, the third count was always the same as one of the first two counts and was thus used for ageing. The level of precision of the final counts for a subsample of 200 otoliths covering a wide size range of fish was assessed by comparing these counts with those obtained independently for the same otoliths by an experienced reader of otoliths (P. Coulson). The resultant overall coefficient of variation of 3.7% was below the 5% reference level regarded as an acceptable level of agreement by Campana (2001).

The trends exhibited by the mean monthly marginal increments (MIs) on otoliths were then used to validate that a single opaque zone is typically formed annually in the otoliths of *P. octolineatus*. The MI is defined as the distance between the outer edge of the single or outermost opaque zone of the otolith and the periphery of the otolith. The MI was expressed as a proportion of either the distance between the primordium and the outer edge of the single opaque zone in otoliths with only one zone, or as the distance between the outer edges of the two outermost opaque zones in otoliths with two or more such zones. All distances were measured to the nearest 0.01 mm (using Leica Application

Suite ver.3.0) and along the same axis on the anterior side of the otolith near the sulcus and perpendicular to the opaque zones.

Each individual was assigned an age based on its date of capture, the number of opaque zones in its otolith, the time of year when opaque zones typically become delineated from the otolith periphery and a designated 'birth' date of 1 December, which represents the approximate midpoint of the spawning period (see Results).

Growth

The lengths at age of small *P. octolineatus*, i.e. <100 mm in Mangles Bay, whose sex could generally not be determined macroscopically, were assigned randomly, but in equal proportions, to the female and male datasets. The traditional von Bertalanffy growth curve was fitted separately to the lengths at age of fish. The curve is:

$$L_j = L_\infty \{1 - \exp(-[k(t_j - t_0)])\}$$

where L_j represents the length of the j th fish, which has age t_j , L_∞ is the asymptotic length, k is the von Bertalanffy growth coefficient and t_0 is the age at which the length of the fish is expected to be zero.

Because the lengths at age of the older fish approach the asymptote more rapidly than predicted by the traditional von Bertalanffy curve (see Results), this growth model was enhanced to allow for a linear increase in the growth coefficient (k) with increasing age (i.e. $k_j = k_1 + k_2(t_j - t_0)$). The resultant enhanced growth model was:

$$L_j = L_\infty \{1 - \exp(-[(k_1 + k_2[t_j - t_0])(t_j - t_0)])\}$$

Because plots of the distribution of the lengths v. age of *P. octolineatus* showed that growth was seasonal, the above model was extended by modifying the seasonal growth model of Somers (1988) to allow for the proposed linear trend in k with respect to age. Thus, with a slight change in the symbols used:

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

where L_j and t_j are the respective length and age of fish j , $S(t) = \sin[2\pi(t - t_c)]$, C is a constant and t_c serves as the phase that shifts the sine curve (SC) with respect to the age t . That is, t_c determines the time within the year at which growth is at a maximum or minimum. In this model, the seasonality amplitude parameter (C) is constrained to values between 0 and 1.

The three growth models, i.e. traditional von Bertalanffy growth model, enhanced von Bertalanffy growth model and the SC-based seasonal model, were all fitted to the lengths at age of (1) females, (2) males and (3) all fish by minimising the negative log-likelihood (NLL) using the software program, R (R Core Team 2012). Values of the Akaike Information Criterion (AIC) were calculated from the NLL and number of parameters K as $AIC = 2NLL + 2K$ (Burnham and Anderson 2002) for comparing the above fits to the lengths at age derived using the three growths curves and also a temperature-based seasonal growth model (see Supplementary material). Instantaneous rates of change in length with age were calculated from the fitted growth curves for ages covering the observed age ranges for *P. octolineatus*. All growth models were constrained to ensure that growth rates did not become negative, i.e. fish did not 'shrink' (McGarvey and Fowler 2002). Trends in residuals from the fitted models were examined to assess whether the curves adequately described the distributions of the lengths at age. A bootstrapping analysis was undertaken within the software package R for these datasets, by drawing 200 random samples (with replacement) from the data and refitting the model. The 2.5 and 97.5 percentiles of the resulting parameter estimates were accepted as approximate 95% confidence limits for the parameter. Likelihood-ratio tests were used to compare the three growth models for each sex and the growth of females and males.

Reproduction

The gonads of each *P. octolineatus* >100 mm were removed, weighed to the nearest 0.01 g and, on the basis of their macroscopic appearance, assigned to one of the following maturity stages, based on the criteria of Laevastu (1965): I = virgin, II = immature or resting, III = developing, IV = maturing, V/VI = prespawning/spawning, VII = spent, VIII = recovering/spent. The cut-off point of 100 mm was chosen as it was the approximate length above which all fish could be sexed. Note that stages V and VI were combined as it is sometimes not possible to distinguish between these two stages

macroscopically, i.e. when either or both migratory nucleus stage oocytes and post-ovulatory follicles, but not hydrated oocytes, are present.

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. These gonads were thus placed in Bouin's fixative for 24–48 h, depending on their size, and then dehydrated in a series of increasing concentrations of ethanol. The mid-region of these gonads were embedded in paraffin wax and cut into 6- μ m transverse sections, which were mounted on microscope slides, stained with either Mallory's trichrome or Ehrlich's haematoxylin and eosin and examined using a compound microscope.

The gonadosomatic index (GSI) of each female and male greater than or equal to their respective total length at which 50% of *P. octolineatus* attain maturity (TL₅₀) (i.e. 141 and 131 mm TL respectively, see Results) was calculated as:

$$\text{GSI} = M_G/M \times 100$$

where M_G is the mass of the gonad (g) and M the total mass of the fish (g). The resultant GSIs for both the females and males in each calendar month of the year were pooled and the mean monthly values and their standard errors then calculated for each sex.

Length and age at maturity

The lengths at which 50 and 95% of female and male *P. octolineatus* attain maturity (TL₅₀ and TL₉₅ respectively), and their 95% confidence limits, were determined by logistic regression analysis. For this analysis, a fish caught during the spawning period was considered to possess 'mature' gonads when its gonads were at one of stages III–VIII, which assumes that such fish were destined to become mature or had already reached maturity during that period (see Results). The probability (P) that a female or male *P. octolineatus* of length TL was mature was determined as:

$$P = \{1 + \exp[-\ln(19)(\text{TL} - \text{TL}_{50})(\text{TL}_{95} - \text{TL}_{50})^{-1}]\}^{-1}$$

This model was fitted by maximising the likelihood within R. Resampling with replacement, similar to that described for the growth analyses, was employed to determine the 95% confidence limits for the logistic parameters.

Results

Water temperature and salinity

Mean monthly salinities in the marine bays remained similar throughout the year, ranging between 32.4 and 36.5, reflecting winter runoff in the first case and high evaporation rates in the second (data not shown). Mean monthly water temperatures in these bays increased from a minimum of 14.2°C in July to a maximum of 25.1°C in February and then declined sequentially in the ensuing months (Fig. 2a). Mean monthly daylight hours rose from their minimum value of 10.1 h in July to peak at 14.2 h in December and then declined to 10.3 h in June (Fig. 2b).

Validation of ageing

The region surrounding the primordium of the otolith of *P. octolineatus* is large and opaque and the first translucent zone is wide and diffuse. The otoliths of the new 0+ recruits, caught at lengths of 15–55 mm in mid-summer (January) at the end of the spawning season, did not contain an opaque zone outside that translucent zone and this was also true for those of the corresponding cohort in the ensuing months, whose lengths remained discrete in sequential monthly length–frequency distributions (see later in Results). An opaque zone was first detected near the periphery of the otoliths of a few individuals in early summer (December), by which time the fish had reached 74–93 mm and represented individuals at the beginning of their second year of life. The first opaque zone is thus laid down during the first winter and early spring of life. Alternating opaque and translucent zones were clearly visible in sectioned otoliths of *P. octolineatus*, with the opaque zones (annuli) best defined on the anterior side of the otolith.

The mean monthly MIs for otoliths with one opaque zone declined precipitously from a maximum of 0.28 in November to a minimum of 0.14 in January and then increased progressively during the ensuing months (Fig. 3). The trends exhibited throughout the year by the mean monthly MIs for otoliths with a greater number of opaque zones were similar, but declined to their minima slightly later, i.e. in February for otoliths with two or three zones and in March with those with greater than or equal to four opaque zones (Fig. 3). The single pronounced decline and then rise in the mean monthly MIs of otoliths, irrespective of the number of opaque zones, demonstrates that a single opaque zone is typically formed each year in the otoliths of *P. octolineatus* and that the number of such zones in these otoliths can thus be used for ageing this species.

Abundance and length and age compositions

The mean number of *P. octolineatus* caught using the 21.5-m seine net in the dense seagrass beds of shallow waters in Mangles Bay was relatively low in summer and then rose markedly in autumn following the completion of spawning, reflecting the recruitment of large numbers of new 0+ recruits into these sheltered waters (Fig. 4). The mean numbers declined in winter and increased only slightly in spring. Although the mean number of *P. octolineatus* recorded in autumn was far greater than in all other seasons, the catches in this month were highly variable, which accounts for the one-way ANOVA ($P > 0.05$) failing to detect a significant difference among this and other seasons. The mean TL of *P. octolineatus* increased from 47 mm in summer to 60 mm in autumn, and remained at about this value during winter, before rising to 66 mm in spring (Fig. 4).

The TL of the *P. octolineatus* caught in the shallows of Mangles Bay ranged from 12 to 162 mm ($x = 57$ mm), with most measuring <100 mm and producing a modal length class of 50–74 mm (Fig. 5a). The samples were dominated by 0+ fish (94%) and contained only a few 1+ fish and one 2+ fish (Fig. 5b). The TL of female and male *P. octolineatus*, caught by rod and line in offshore waters of Mangles Bay and Safety Bay collectively, ranged from 124 to 256 mm ($x = 195$ mm) and 113–240 mm ($x = 186$ mm) respectively. Although the modal length class of females and males was the same, i.e. 175–199 mm, the proportion of females in each length class was always greater than that of males (Fig. 5c). The majority of both sexes caught by rod and line belonged to the 1+ to 3+ age classes and

produced a prominent modal age class of 2+ years (Fig. 5d). The samples also contained, however, several 4+ to 6+ fish and a few 7+ to 10+ fish. The maximum ages of female and male *P. octolineatus* were 10.2 and 9.2 years respectively.

The 0+ cohort of *P. octolineatus* was first caught in the seagrass meadows of Mangles Bay in December, when it was represented by a few fish with lengths of only 12–19 mm, the former being essentially the length at which this species metamorphoses (Neira *et al.* 1998), and then by far larger numbers in subsequent months (Fig. 6). The modal length class of that cohort in the seine net samples increased from 20–29 mm in January to 50–59 mm in April, where it remained until October, before increasing to 60–69 mm in November and then markedly so to 80–89 mm in December as the fish became 1+ years old. The trends exhibited by the modal length classes in sequential monthly length–frequency distributions thus demonstrated that growth is seasonal during the first year of life. The seine net samples contained only a few 1+ fish in January and February and none in subsequent months (Fig. 6). The trends just described for 0+ fish in seine net catches were derived largely from fish <100 mm and could not thus typically be sexed. They therefore represented the fish that had been assigned randomly and alternately to the female dataset, the other fish having been assigned to the male dataset. Naturally, the trends exhibited by the 0+ fish assigned to the male dataset were very similar (Veale 2013).

The 1+ age class of female *P. octolineatus* was caught in variable numbers by rod and line in the deeper waters of Mangles Bay and Safety Bay in every month except December and January (Fig. 6). In months when 1+ fish were abundant, the midpoint in the length range for that age class within the length–frequency distribution lay to the left of that for the 2+ fish, which in turn was to the left of that for the 3+ year class, but with the length distributions of successive age classes showing considerable overlap. The monthly length–frequency distributions of males (not shown) were similar to those of females. The presence of only a small number of individuals in the length range of 100–140 mm TL, in samples caught collectively by seine net in dense nearshore seagrass and by rod and line in waters further offshore, is presumably a function of gear selectivity. Unfortunately, this assumption could not

be tested because it was not possible to sample either the dense seagrass with rod and line because of snagging of the hooks or the offshore waters with the seine net because the depth was too great.

Growth

The traditional von Bertalanffy growth curve passed above the points for the older females of *P. octolineatus* (Fig. 7a) and the same was true for males (Veale 2013). Although the enhanced von Bertalanffy curve resolved this problem at the upper end of the growth curves (Fig. 7b), it did not describe the seasonal changes in growth that were clearly apparent from the trends exhibited by the modal length of particularly the young fish in sequential monthly samples (Fig. 6). The SC-based seasonal growth model captured the seasonal changes in the lengths at age of females (Fig. 7c) and also of males (Veale 2013). Comparisons between the residual plots (Figs 7d,e,f) and AIC values for the seasonal growth models for females and males and those for the traditional and enhanced von Bertalanffy curves for the corresponding sexes demonstrated that, after taking the number of parameters in the models into account, the fits to the lengths at age of both sexes were improved by using a growth curve that accommodated a seasonal effect (Table 1). This conclusion was confirmed by the results of the likelihood-ratio tests, which compared the first two models with the latter model (all $P < 0.001$). Note that a temperature-related seasonal growth curve was also developed and fitted to the lengths at age of *P. octolineatus*, and that this produced very similar estimates of expected lengths at age as those calculated using the SC-based seasonal growth curve. However, based on the values of the AICs of the two models and their numbers of parameters, this temperature-related seasonal growth curve did not improve the fit of that model (see Supplementary material). The SC seasonal growth model is thus used for subsequent comparisons of the growth curves for each sex.

The growth of the females and males of *P. octolineatus* differed significantly ($P < 0.001$), which is reflected in the fact that, on average, the TLs estimated using the SC seasonal growth model at ages 2, 3, 4 and 6 years were slightly greater for females, i.e. 157, 197, 211 and 214 mm, than for males, i.e. 153, 188, 200 and 202 mm. The differences between the sexes at these ages, which were only 2.5, 4.5, 5.4 and 5.6% respectively, are reflected in slightly higher estimates of L_{∞} for females than males (Table 1). The SC seasonal growth model demonstrated that most of the growth occurs between

October and March, i.e. mid spring to early autumn and during the first 3 years of life, by the end of which time both sexes have reached ~90% of their respective maximum lengths.

The instantaneous daily growth rates of females and males, predicted by the SC seasonal model, underwent similar and very pronounced seasonal changes, peaking in summer and declining to a minimum in winter (Fig. 8). The maximum daily growth rate of females, employing the SC growth model, was greatest at ~age 1 year, i.e. ~0.35 mm day⁻¹, and subsequently declined with increasing age. Note that, as spawning occurs in summer, the new 0+ recruits did not appear in substantial numbers until late in that season (Fig. 8). The trends exhibited by the males (Veale 2013) were very similar to those of females.

Gonadal recrudescence and spawning

The mean monthly GSI for females and males with lengths \geq their respective values for the TL₅₀ at maturity, rose progressively and markedly after August to reach a sharp peak in December and then fell precipitously to low levels in March (Fig. 9). Fish with stage III (developing) and stage IV (maturing) ovaries and testes were found between August and January, whereas those with gonads at stage V/VI (mature/spawning) were largely confined to October to February and those at stage VII (spent) to February and March (Fig. 9). The approximate midpoint of the spawning period was November–December, and thus 1 December was selected as the ‘average’ birth date for *P.*

octolineatus.

Lengths and ages at maturity

During the main part of the spawning period (November to January), the smallest mature female and male *P. octolineatus* were 137 and 134 mm respectively, recognising, however, that the number of fish in the 120–129 mm length class was small (Fig. 10). The percentage of mature female *P. octolineatus* increased from ~65% in fish with TLs of 130–139 mm to 100% in females >190 mm TL. All but two males with TLs >130 mm were mature (Fig. 10). The TL₅₀ values for female and male *P. octolineatus* were 140 and 131 mm respectively (Table 2). Maturity was attained by a few males and

females during their first year of life and typically by all fish at the completion of their second year of life (Fig. 10).

Discussion

Habitats, movements, age and size compositions

Because 0+ *P. octolineatus*, with lengths of 12–20 mm TL, were caught in the dense seagrass in Mangles Bay and this terapontid metamorphoses at 11 mm (Neira *et al.* 1998), at least a number of this species settle in these meadows soon after becoming juveniles. Furthermore, because the very large catches of *P. octolineatus* in this seagrass comprised 0+ and early 1+ fish and measured <100 mm TL, which is well below the minimum TL of 134 mm of either sex at maturity, seagrass constitutes an important nursery area for this terapontid in coastal marine waters. This conclusion is consistent with this habitat type being the only one to yield substantial numbers of juvenile *P. octolineatus* during extensive sampling of a range of habitats in marine waters along the lower west coast of Australia (Valesini *et al.* 2004). Furthermore, *P. octolineatus* (previously erroneously referred to as *P. sexlineatus* in Western Australia) was caught only in vegetated habitats when trawling shallower waters in Shark Bay, over 800 km to the north of the study area (Travers and Potter 2002). Seagrass meadows also provide an important nursery habitat for its congener *P. sexlineatus* in south-eastern Australia and several other fish species in south-western Australia, such as the tarwhine *Rhabdosargus sarba*, the western trumpeter whiting *Sillago berrus* and older juveniles of the King George whiting *Sillaginodes punctatus* (Smith and Suthers 2000; Hesp *et al.* 2004; Valesini *et al.* 2004).

In contrast to the situation with nearshore seagrass meadows in Mangles Bay, the substantial catches of *P. octolineatus* taken by rod and line in patchy seagrass in the immediately offshore, deeper waters of this bay contained exclusively 1+ and older fish that ranged up to 10 years old, and that typically exceeded 140 mm in length. It is thus concluded that, in Mangles Bay, *P. octolineatus* moves into sparser seagrass beds in offshore, deeper waters when it is ~1 year old and has attained lengths

approaching 100 mm and where, from the presence of large numbers of all maturity stages, it subsequently matures. Although it is not clear whether some of the adults in Safety Bay are also derived from juveniles in Mangles Bay, the biological characteristics of the adults in both bays are essentially the same. Because there are large gaps between dense seagrass areas along the Western Australian coast, it seems likely that the assemblages in Mangles Bay–Safety Bay and Shark Bay, at a far lower latitude, represent different populations.

Seasonal growth

Our data demonstrate that *P. octolineatus* has moderate longevity (maximum age of 10 years) and grows rapidly towards its asymptote, with females and males reaching ~90% of their maximum TLs by the end of their third year of life. The enhancement of the von Bertalanffy growth curve to allow for a linear increase in the growth coefficient with age improved the fit to the lengths at age of both the older females and males of *P. octolineatus*. However, the SC-based growth model provided an even better fit than the enhanced von Bertalanffy growth curve by accommodating the well defined seasonal pattern of growth. Such seasonality in growth, which is also exhibited by another terapontid, i.e. *A. caudavittata* in the nearby Swan–Canning Estuary (Wise *et al.* 1994), is a common feature of growth in ectotherms (García-Berthou *et al.* 2012). The pronounced seasonality in growth of *P. octolineatus* is further emphasised by the fact that the instantaneous daily growth rates of the females and males both peaked during mid-summer.

The highly seasonal pattern of *P. octolineatus* in coastal marine waters of temperate south-western Australia strongly suggests that the growth of this species is influenced by water temperature. This view is consistent with the growth of *P. octolineatus* being negligible from April to October, when the mean monthly water temperatures in these waters were lowest, i.e. 14–21°C, and substantial between November and March, when water temperatures were elevated, i.e. 21–25°C. The evidence that growth is correlated with temperature is supported by the fact that a temperature-related growth curve also provided a good fit to the lengths at ages of *P. octolineatus* (see Supplementary material), recognising however, that it did not improve the fit provided to the data by the SC-based seasonal growth curve.

Mean monthly water temperatures at ~18°S, the northernmost limit of the distribution of *P. octolineatus* (Gomon *et al.* 2008), typically range from 21 to 31°C (CSIRO 2003). Thus, because water temperatures in the study area at 32°S at the southern end of this distribution (Hutchins and Swainston 1986) are far lower (i.e. from 14 to 25°C), the highly seasonal growth of this species at these higher and cooler latitudes probably reflects the limited period over which water temperatures are sufficiently warm to be conducive for growth. Thus, faster growth of *P. octolineatus* during the warmer months in south-western Australian waters may compensate for shorter optimal growing periods in this region. This evolutionary response, known as ‘countergradient variation’ (Conover and Present 1990), has been described for other species elsewhere in the world, e.g. Atlantic silversides *Menidia menidia* (Yamahira and Conover 2002), Atlantic halibut *Hippoglossus hippoglossus* (Jonassen *et al.* 2000) and grey snapper *Lutjanus griseus* (Denit and Sponaugle 2004). This is often considered to reflect selection for characteristics that facilitate the rapid attainment by individuals of a large body size and thereby an increased chance of survival during their first winter (Levins 1969; Power and McKinley 1997; Jonassen *et al.* 2000).

Because *A. caudavittata* occurs from south-western Australia, where it is confined to estuaries (Potter *et al.* 1994; Wise *et al.* 1994), to northern Australia and southern New Guinea to the east coast of northern Queensland (Vari 1978; Allen *et al.* 2002), its seasonal growth in the Swan–Canning Estuary may also be related to the greater seasonal changes in water temperature at this latitude.

Reproductive biology

As *P. octolineatus* with stage III gonads first appeared in the samples from August, gonadal recrudescence commences in this month and thus as temperature and light regimes have started to increase. This parallels the trend for gonadal recrudescence in numerous temperate fish species to be ‘triggered’ by a combination of increases in these two environmental variables (Lam 1983). Such species include other terapontids, i.e. *A. caudavittata* in the nearby Swan–Canning Estuary (Fig. 1; Potter *et al.* 1994) and the spangled perch *Leiopotherapon unicolor* (formerly *Therapon unicolor*) in freshwater rivers and lakes in northern Australia (Beumer 1979).

The progressive and marked rise in the mean monthly GSIs for *P. octolineatus* in offshore waters of the marine bays between October and November and their subsequent sharp peak in December and progressive decline between January and April demonstrate that this species has a highly seasonal spawning period. As most of the *P. octolineatus* with stage V/VI (pre-spawning/spawning) ovaries and testes were caught between October and January and those with stage VII (spent) gonads were largely confined to February and March, *P. octolineatus* spawns predominantly between mid-spring and mid-summer. This spawning period, which occurs when mean monthly water temperatures were ~23°C and close to their maxima, is similar to that of *P. sexlineatus* (Smith and Suthers 2000) and other terapontids in Australian waters, i.e. *A. caudavittata* (Potter *et al.* 1994) and *L. unicolor* (Beumer 1979).

The trends exhibited by the prevalence of mature gonads in *P. octolineatus* of different ages demonstrate that a few individuals are capable of spawning at the end of their first year of life, and that this is essentially true of all individuals by the end of their second year, which parallels the situation with *A. caudavittata* in the Swan–Canning Estuary (Potter *et al.* 1994). Furthermore, as mature gonads were found in fish at the end of each of their third to eighth years of life, some individuals mature and spawn in several successive years.

In summary, the results of this study provide the first detailed information on the life cycle of a terapontid, which are based on sound ageing of individual fish and on samples collected at regular intervals from the nearshore shallow and offshore deeper habitats of this species. The results thus substantially enhance our knowledge of a family that is speciose, abundant and widely distributed in the Indo-West Pacific. Although *P. octolineatus* is very abundant in the seagrass beds off the lower western coast of Australia, there is no indication that exploitation will increase substantially in the near future. *Pelates octolineatus* undertakes a size- and age-related movement from shallow, nearshore dense seagrass to deeper, offshore and sparser seagrass, where it matures and spawns, and thus may be classified as a ‘permanent resident’ of seagrass habitat (*sensu* Jackson *et al.* 2001). The depth-related changes in the distribution of *P. octolineatus* parallel the movements of several other species in the coastal marine waters of south-western Australia such as *R. sarba*, the southern school

whiting *Sillago bassensis* and *S. punctatus* (Hyndes *et al.* 1996, 1997; Hesp *et al.* 2004), and by several species elsewhere (e.g. Werner and Gilliam 1984; Griffiths and Wilke 2002; Meyer and Holland 2005). Such movements reduce the potential for intraspecific competition for spatial and food resources.

Because *P. octolineatus* was the most abundant of the fish species caught in *Posidonia sinuosa* during the present study and in coastal waters along the lower west Australian coast (Valesini *et al.* 2004; Wakefield *et al.* 2013), this species clearly plays a major role in the structure and function of seagrass meadows in these waters and the same is likely to be true for its congener *P. sexlineatus* in south-eastern Australia (Smith and Suthers 2000). Such a view is consistent with the fact that, in Shark Bay, over 800 km further north, *P. octolineatus* was the dominant grazer of seagrasses in the extensive meadows of a sub-tropical embayment, where this omnivore consumes whole blades and is considered likely to play a significant role in removing leaf tissue from the abundant seagrass species *Halophila spinulosa* (Burkholder *et al.* 2012). This parallels the high levels of herbivory by *Sarpa salpa* in the Mediterranean Sea (Pagès *et al.* 2012) and *Leptoscarus vaigiensis* in Indo-Pacific waters (Unsworth *et al.* 2007), and the strong influence of these dominant grazers on the structure and function of their associated seagrass ecosystems. One of the most striking features of *P. octolineatus* on the lower western Australian coast is its marked seasonal pattern of growth, presumably reflecting the limited period in which water temperatures are conducive to growth. It is thus relevant that the temperatures in these waters range more widely between summer and winter and only approach, for a relatively short period, those found in lower latitudes further north in the main part of the distribution of this essentially sub-tropical species.

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Fig. 1. Maps showing the sampling region in western Australia (denoted by arrow in box) and the locations in which *Pelates octolineatus* was sampled and particularly in Mangles Bay and Safety Bay. The arrows in Mangles Bay and Safety Bay identify the midpoints of the ~1 km long stretches sampled in those bays.

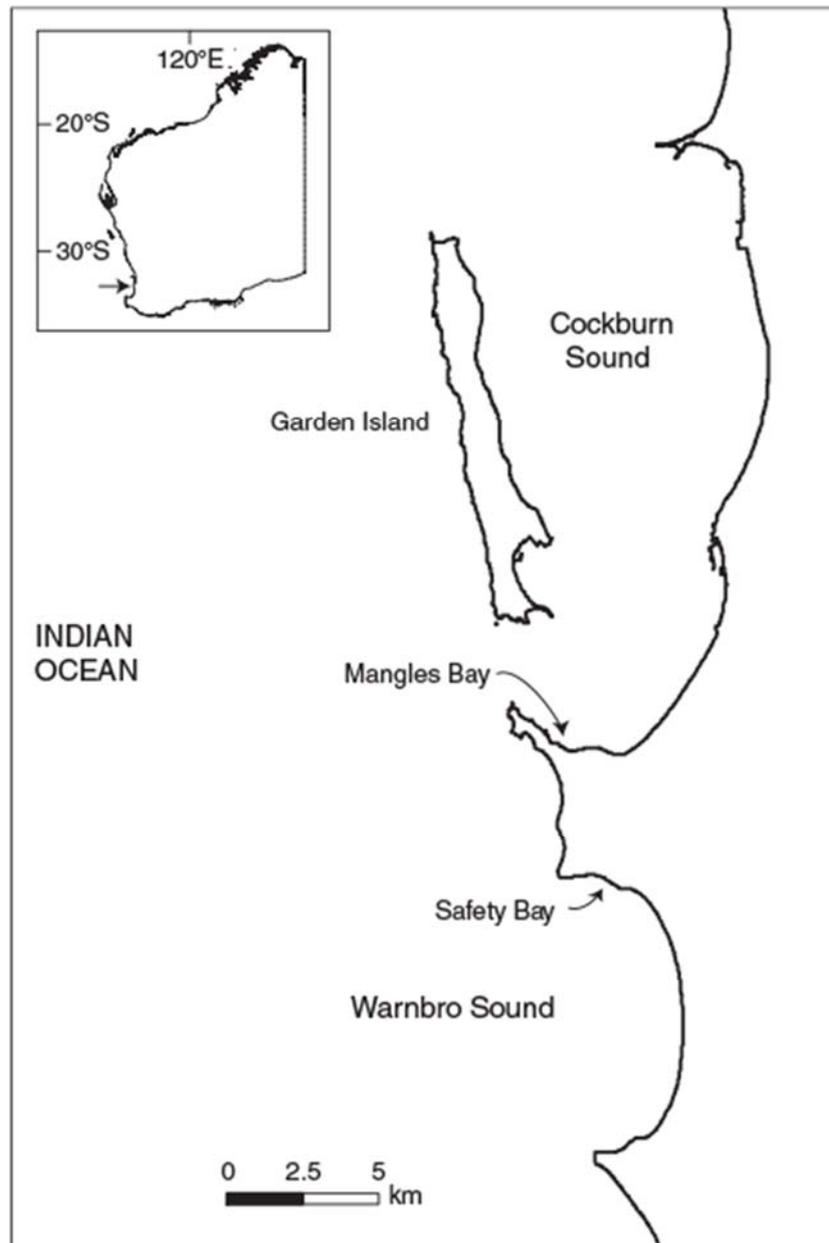


Fig. 2. (a) Mean water temperature in Mangles Bay and Safety Bay ± 1 s.e. and (b) mean daylight hours ± 1 s.e. in the sampling region. Mean temperatures for each calendar month were derived from measurements made on the different sampling occasions in each month between March 2009 and February 2011. Mean monthly daylight durations were derived from data for March 2009 to February 2011, which were extracted from the website www.timeanddate.com. Closed rectangles on the x-axis refer to winter and summer months and open rectangles to spring and autumn months.

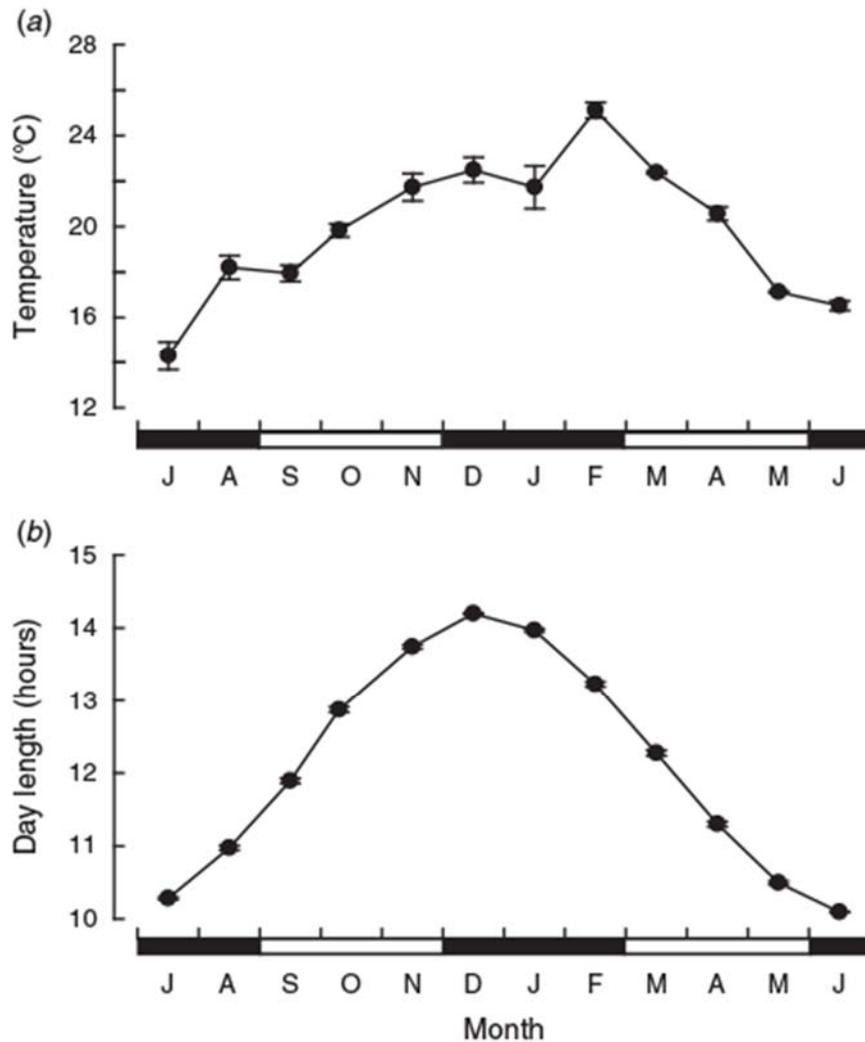


Fig. 3. Mean monthly marginal increments ± 1 s.e. for sectioned otoliths of *Pelates octolineatus* with different numbers of opaque zones. Sample sizes for each month are shown above each monthly mean. Closed rectangles on the x-axis refer to winter and summer months and open rectangles to spring and autumn months.

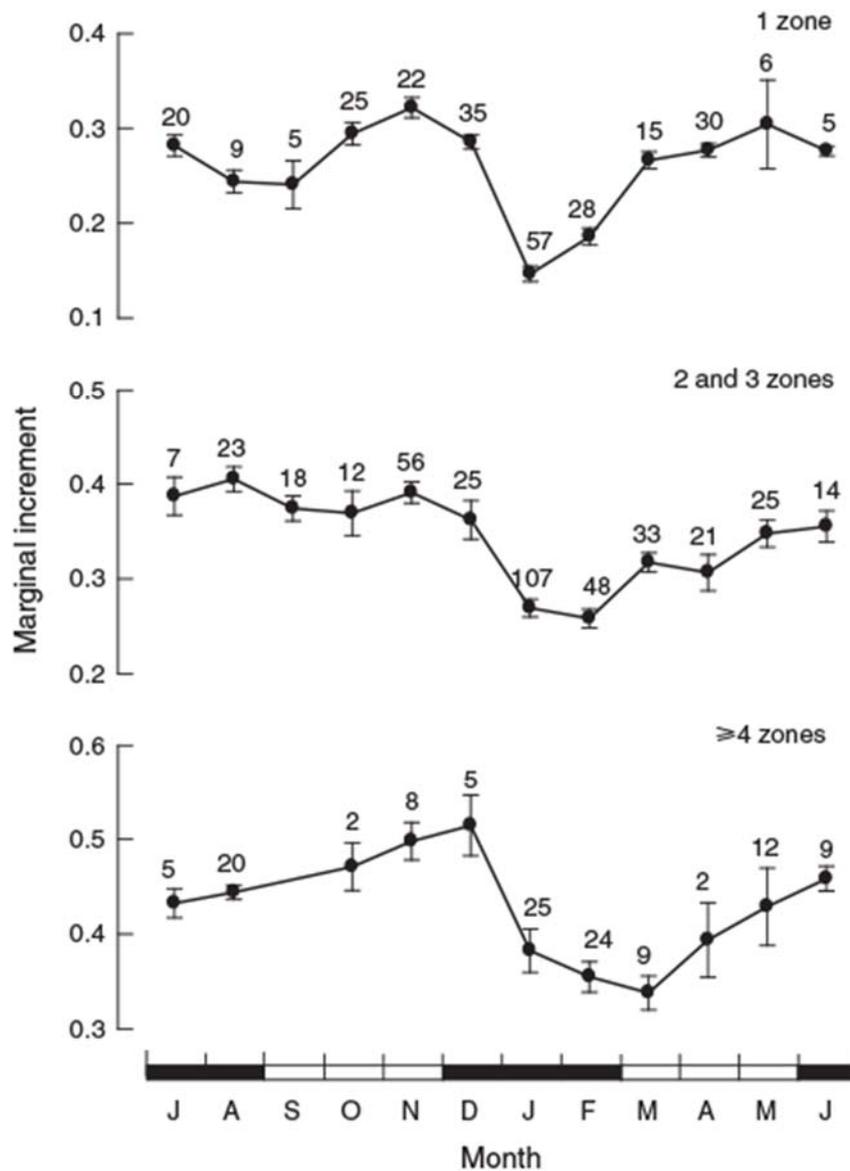


Fig. 4. Mean number of fish per sample (open squares) \pm 1 s.e. and mean total length (closed circles) \pm 1 s.e. of *Pelates octolineatus*, derived from samples obtained using the 21.5-m seine net in nearshore, shallow waters of Mangles Bay in each calendar season between autumn 2009 and summer 2011. The sequence commences in summer when the new 0+ recruits first appear in samples.

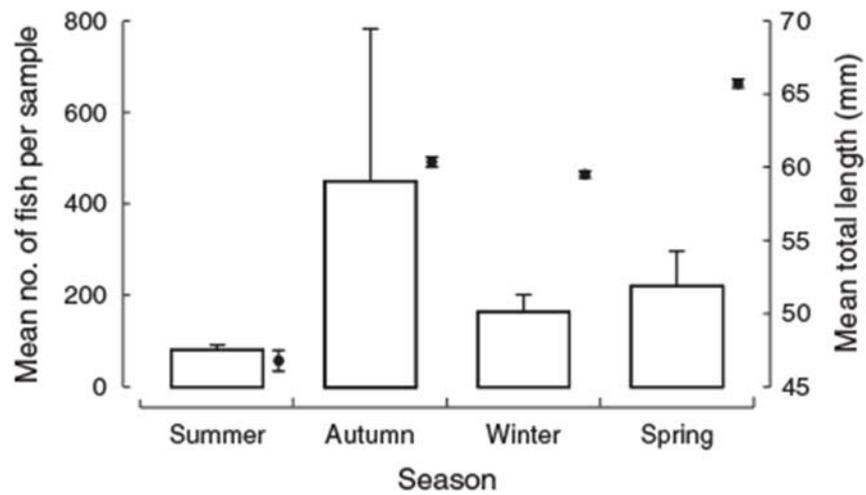


Fig. 5. Length and age-frequency distributions for *Pelates octolineatus* caught by (a, b) the 21.5-m seine net and (c, d) rod and line.

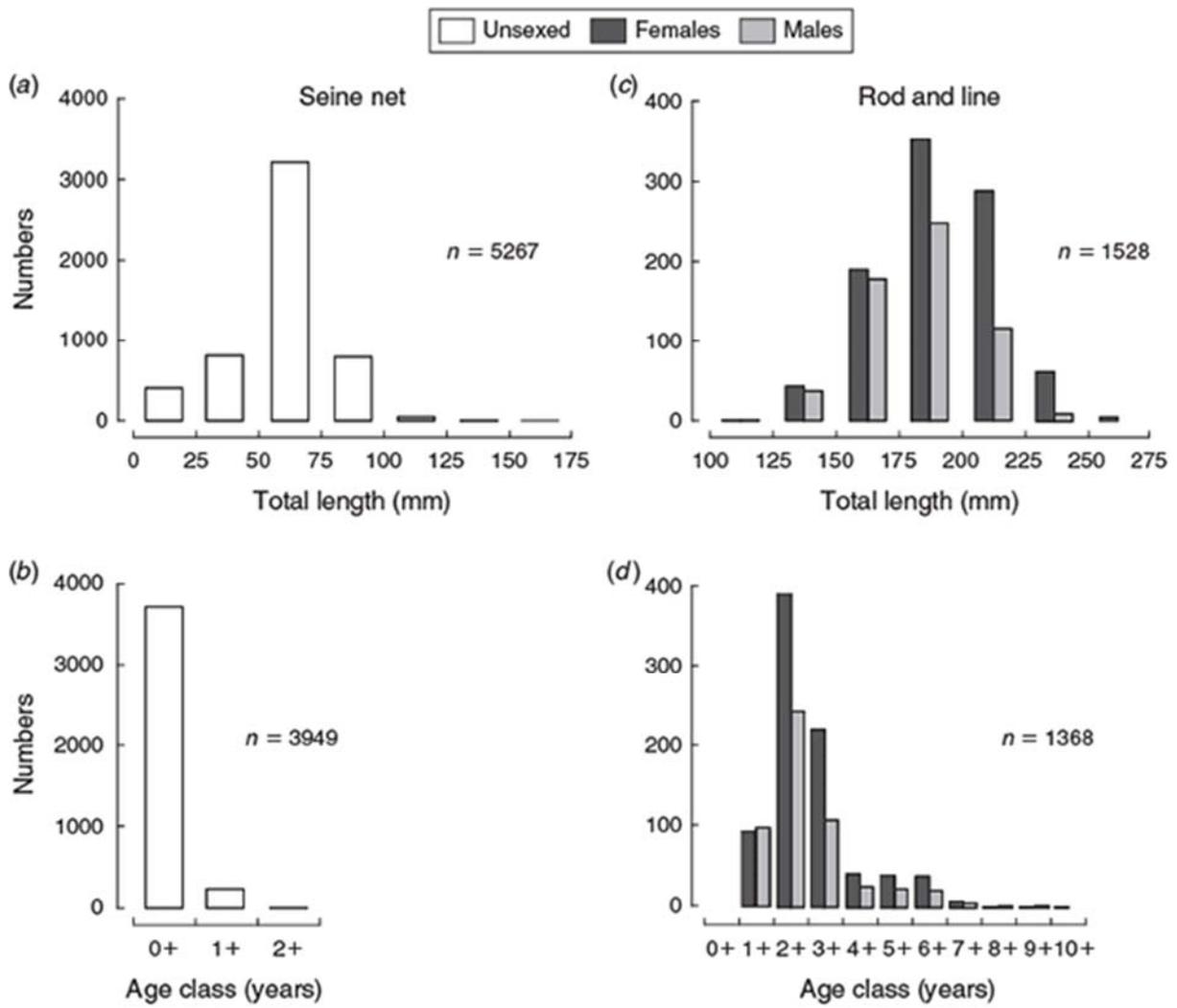


Fig. 6. Monthly length–frequency distributions for different age classes of female *Pelates octolineatus* caught by the 21.5-m seine net and by rod and line. *n*, sample size. Note that, as fish <100 mm TL could not be sexed, they were randomly assigned, in equal proportions, to the female and male datasets and thus those shown in this figure and in Figs 7 and 8 are those assigned as females.

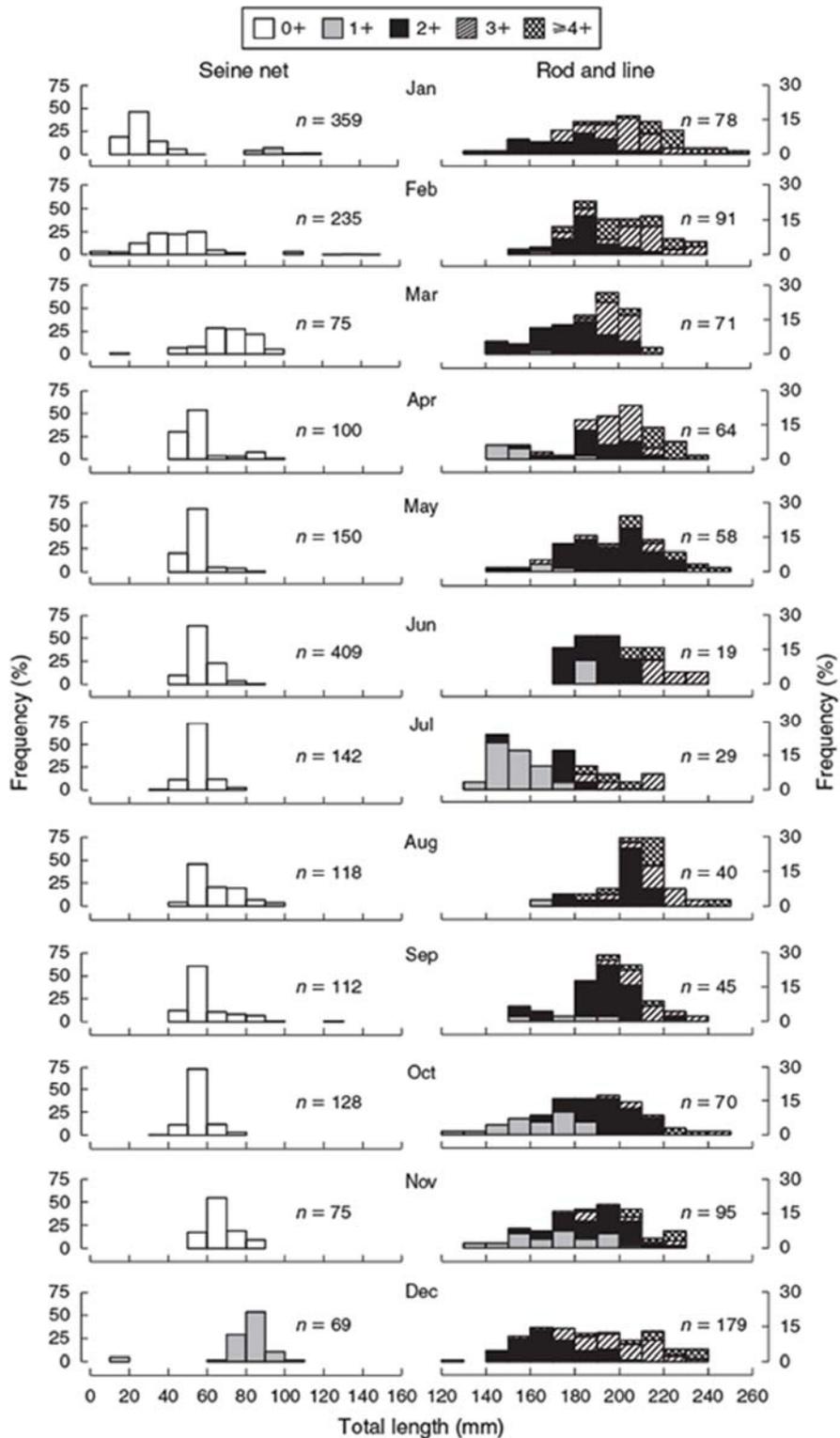


Fig. 7. (a) Traditional von Bertalanffy growth, (b) enhanced von Bertalanffy curve and (c) sine curve-based seasonal growth model fitted to the lengths at age of female *Pelates octolineatus*. The corresponding standardised residuals for each growth curve are shown in (d–f) respectively.

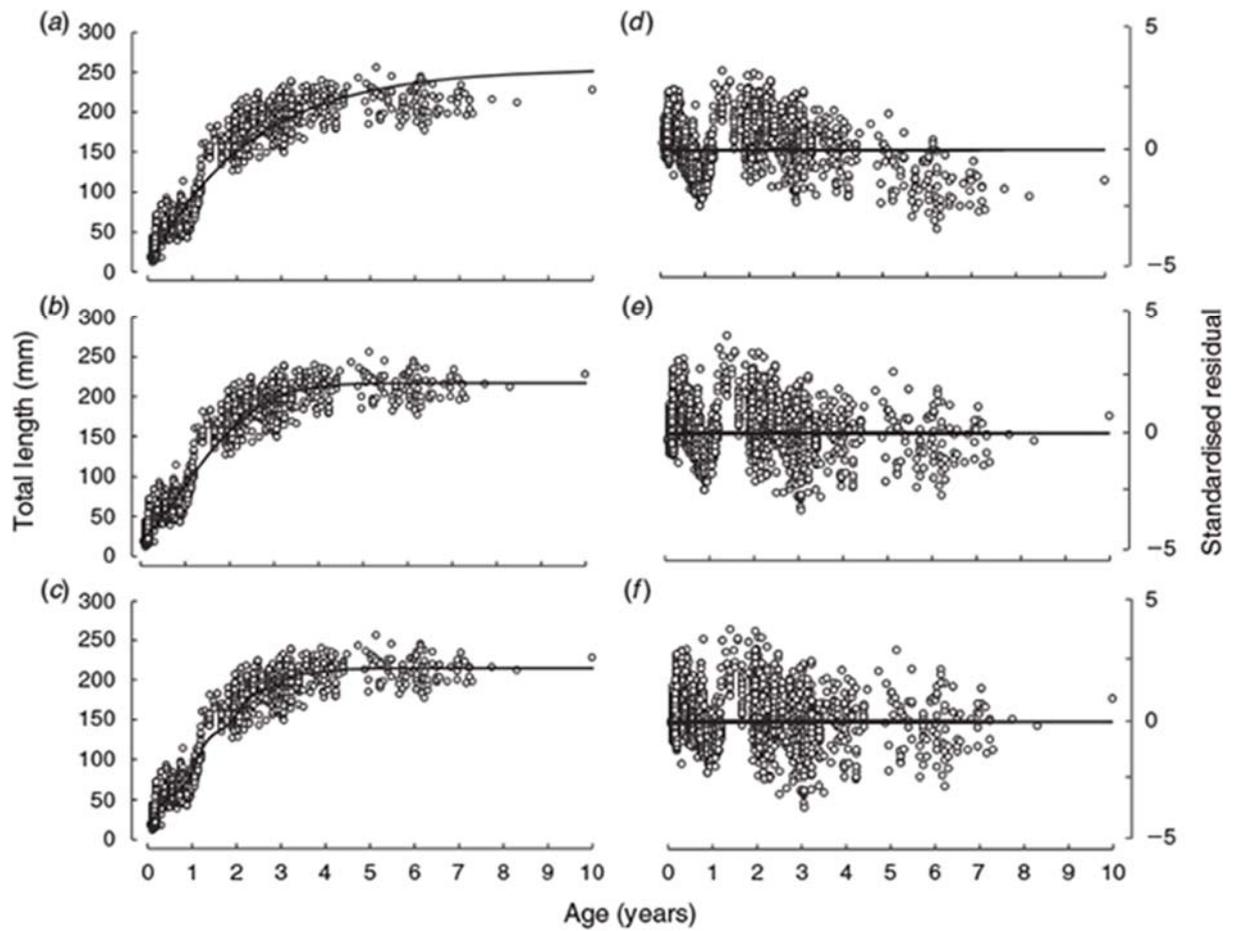


Fig. 8. Relationship between the instantaneous rate of growth and age of female *Pelates octolineatus*, derived using the sine curve-based seasonal growth model.

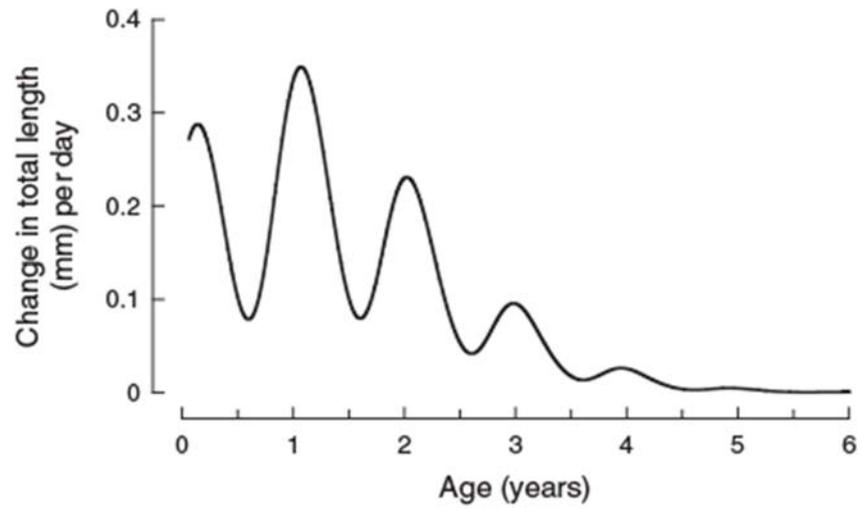


Fig. 9. Mean monthly gonadosomatic indices (GSI) \pm 1 s.e. (black lines) and monthly percentage frequencies of occurrence of stages III–VIII in the gonadal development of female and male *Pelates octolineatus* ($\geq TL_{50}$ at maturity). Sample size for each sex in each month are given. Closed rectangles on the x-axis refer to winter and summer months and open rectangles to spring and autumn months.

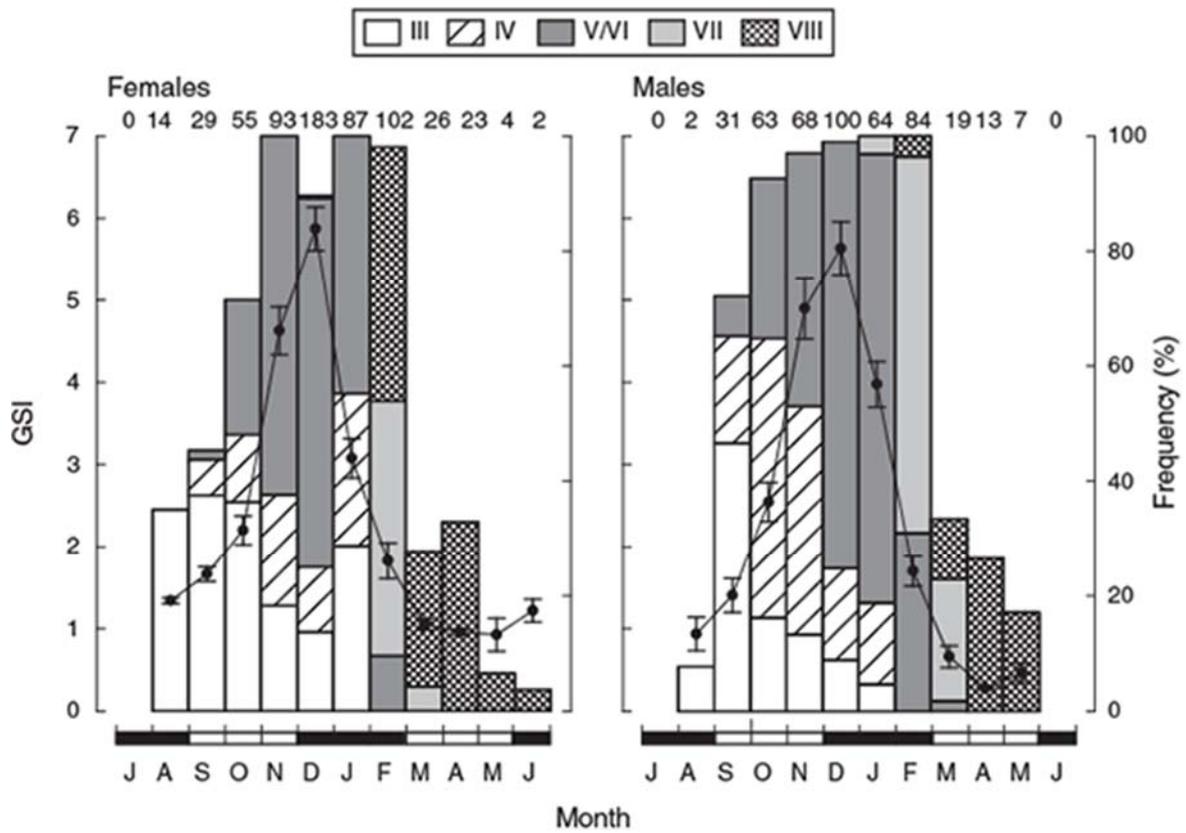


Fig. 10. Percentage frequency of occurrence of (a) females and (b) males of *Pelates octolineatus* with mature gonads, i.e. stages III–VIII (grey histograms), in sequential 10-mm length classes (c, d) at 1, 2, 3 years old, etc., derived from data obtained during the main months of the spawning period. Logistic curves (solid lines) and the $\pm 95\%$ confidence limits (dotted lines) represent the probability that a given fish of a given length is mature. Sample sizes are shown above each bar.

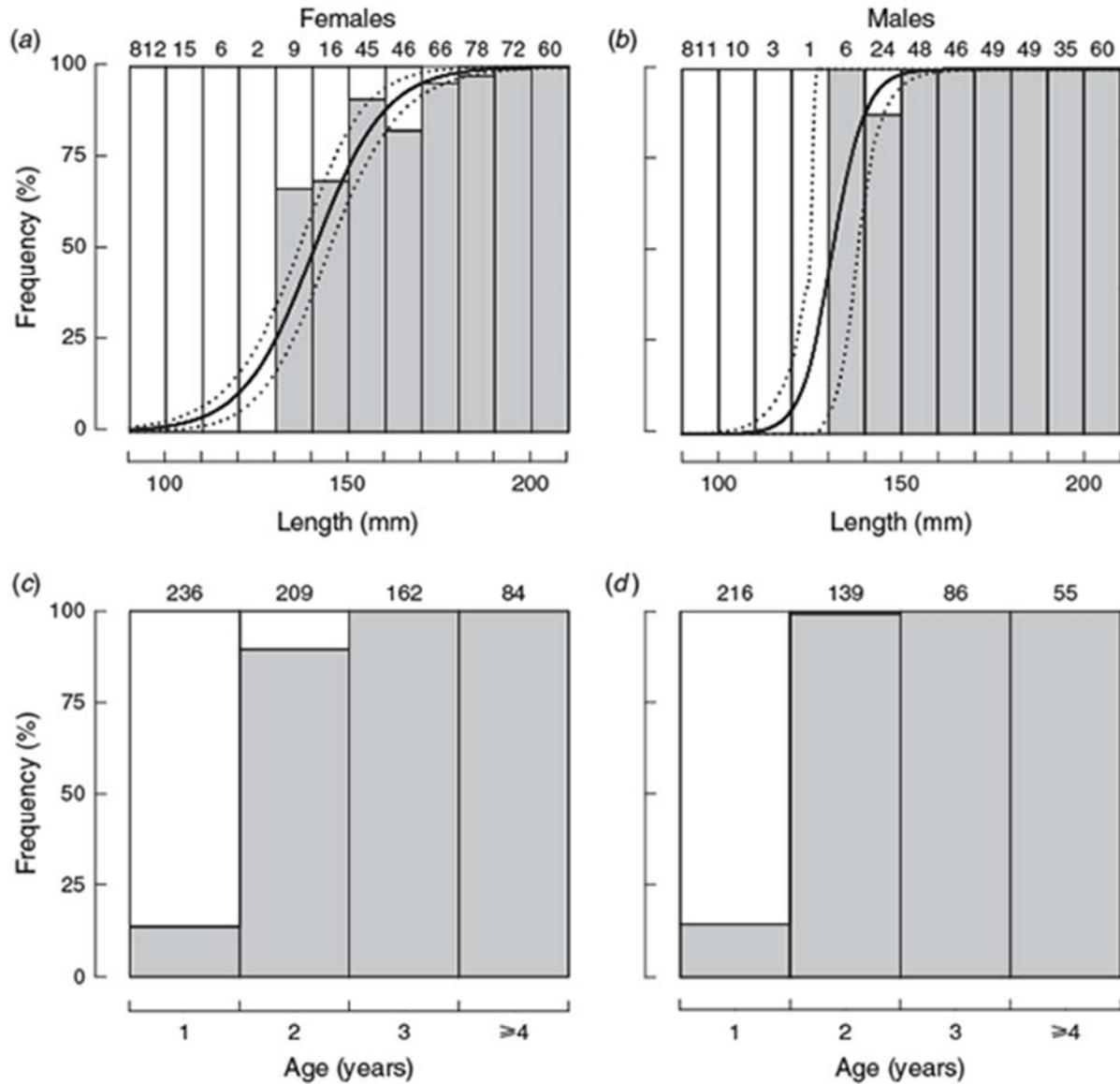


Table 1. Parameters and 95% confidence intervals (CI), negative log-likelihood (NLL) and Akaike's information criterion (AIC) for the fits of the lengths at ages of female and male *Pelates octolineatus* to traditional and enhanced von Bertalanffy growth curves, and the sine curve-based seasonal growth model

L_{∞} is the asymptotic total length (mm), k is the growth coefficient (year^{-1}), t_0 is the hypothetical age (years) at which fish would have zero length, k_1 and k_2 represent the coefficients of the linear relationship of k with age, and C and t_c relate to the seasonality in growth. n , sample size. Note that, taking the number of parameters into account, the model with the lowest AIC provides the best fit

Model	Parameter	Females		Males	
		Estimate	95% CI	Estimate	95% CI
Traditional von Bertalanffy	L_{∞}	255	249, 261	243	237, 249
	k	0.44	0.42, 0.46	0.43	0.41, 0.45
	t_0	-0.07	-0.08, -0.05	-0.10	-0.12, -0.09
	NLL	12 375		10 997	
	AIC	24 759		22 003	
Enhanced von Bertalanffy	L_{∞}	217	217, 217	205	205, 206
	k_1	1.18 E^{-3}	6.45 E^{-4} , 1.13 E^{-2}	1.07 E^{-3}	7.54 E^{-4} , 9.46 E^{-3}
	t_0	-0.75	-0.75, -0.72	-0.78	-0.79, -0.76
	k_2	0.17	0.17, 0.17	0.17	0.17, 0.17
	NLL	11 854		10 606	
Sine curve-based seasonal model	AIC	23 717		21 223	
	L_{∞}	215	212, 217	203	200, 204
	k_1	0.13	0.12, 0.19	0.28	0.26, 0.29
	t_0	-0.44	-0.47, -0.20	-0.10	-0.12, -0.10
	k_2	0.18	0.17, 0.19	0.18	0.17, 0.20
	C	0.99	0.99, 1.00	0.99	0.99, 1.00
	t_c	0.10	0.09, 0.10	0.09	0.08, 0.09
	NLL	11 565		10 326	
AIC	23 144		20 666		

Table 2. Estimates (95% confidence intervals) of the lengths at which 50 and 95% of the females and males of *Pelates octolineatus* attained sexual maturity (TL₅₀ and TL₉₅ respectively) and maximum total length (TL_{max}) and maximum weight (M_{max})

	TL ₅₀	TL ₉₅	TL _{max} (mm)	M _{max} (g)
Females	140 (136, 145)	170 (162, 176)	256	207
Males	131 (126, 138)	144 (127, 150)	240	168