Biology of the harlequin fish *Othos dentex* (Serranidae), with particular emphasis on sexual pattern and other reproductive characteristics

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Key biological characteristics of the harlequin fish *Othos dentex*, a representative of a monospecific genus of the Anthiinae (Serranidae), were determined from samples collected around reefs on the south coast of Western Australia. The females of this relatively long-lived species (maximum recorded age in this study = 37 years) attained only a slightly greater maximum total length and age than males and neither the length nor the age-frequency distributions showed a conspicuous sex-based bimodality. Furthermore, gonads from a wide size and age range of *O. dentex* were shown by histology, at several locations along their length, to always comprise exclusively either ovarian or testicular tissues. Thus, *O. dentex* is a gonochorist, a sexual pattern only previously recorded definitively for one other anthiine serranid, *i.e. Epinephelides armatus*, which also occurs in south-western Australia. Similar to *E. armatus*, *O. dentex* possesses 'solid' testes with a central sperm duct, thereby differing in structure from those typically found in serranids, in which there is a central membrane-bound 'ovarian' lumen and peripherally located sperm sinuses. The gonadal characteristics and sexual pattern of these two gonochoristic anthiines are not consistent with a recent proposal for the trends exhibited by the evolution of gonochorism and protogyny within the Serranidae. *Othos dentex* has indeterminate fecundity and a protracted spawning period (7 months) and, on the basis of underwater observations and a low gonado-somatic index (I_G) for males, is a pair spawner, which is unusual for a gonochorist of a serranid or member of a related family. While the large spots on the lower half of the body of *O. dentex* are shown quantitatively to be similarly yellow in juveniles and adult females, they then become blue in males at maturity and this intensifies during the spawning period, when they presumably play an important role in agonistic interactions among males and courtship with females. The attainment of maturity and rapid growth by *O. dentex* early in life may reflect selection pressures to reduce predation mortality during that period. Total mortality in the population is moderately low during later life, implying that the current fishing pressure on *O. dentex* is relatively light.

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106

INTRODUCTION

The Serranidae were traditionally regarded as comprising three subfamilies, *i.e*. the Anthiinae, Serraninae and Epinephalinae (Hoese *et al.*, 2006; Nelson, 2006). More recently, however, a cladistic study by Smith & Craig (2007) demonstrated that this group is polyphyletic and the Epinephalinae was therefore separated into its own family, the Epinephalidae. The Serranidae *sensu stricto*, comprising the Serraninae and Anthiinae and commonly referred to as sea basses, basslets or hamlets, is a diverse teleost family that is widely distributed in tropical and temperate waters, where it typically lives around coral and rocky reefs (Hoese *et al.*, 2006; Nelson, 2006). The Serraninae contains *c*. 13 genera and 75 species (Nelson, 2006) and the Anthiinae includes at least 21 genera and *c*. 170 species, with both of these subfamilies well represented in Australian waters (Allen *et al.*, 2006; Hoese & Bray, 2006; Nelson, 2006).

In terms of body size, the maximum lengths of serranid species *sensu stricto* range widely (Love *et al.*, 1996; Dulčić *et al.*, 2007; Moore *et al.*, 2007; Gomon *et al.*, 2008). The majority of the ageing studies on serranids that have been based on validated ageing criteria, however, have typically yielded maximum ages of <20 years (Bubley, 2004; Tuset *et al.*, 2004; Moore *et al.*, 2007).

A wide range of sexual patterns is found in the Serranidae, including all forms of hermaphroditism except protandry (Sadovy de Mitcheson & Liu, 2008; Erisman & Hastings, 2011). While certain serranids, such as those belonging to *Paralabrax* species, were initially thought to be protogynous hermaphrodites, examination of the histological characteristics of their gonads revealed that these species are gonochorists (Sadovy & Domeier, 2005). The original conclusion was based on the presence of a prominent, membrane-lined 'ovarian' lumen in the central region of the testes of males. This characteristic may represent a carry-over from the juveniles, which are bisexual, and would account for the sperm sinuses being located on the periphery of these testes. In contrast to the situation with the above gonochoristic serranids, age-frequency data and histological studies of the gonads of breaksea cod *Epinephelides armatus* (Castelnau 1875) demonstrated that, while this anthiine is also a gonochorist, its testes differ from those of the above species in that they do not contain a central 'ovarian' lumen and peripheral sperm sinuses and their central region is occupied instead by a sperm duct (Moore *et al.*, 2007). While *E. armatus* is the only anthiine that has been shown definitively to be gonochoristic, the study by Roberts (1989) suggested that this might also apply to orange perch *Lepidoperca pulchella* (Waite 1899), another species in this subfamily.

The presence of a non-functional, juvenile bisexual phase in the species of the serranine genus *Paralabrax*, in which the testicular and ovarian components are separated (and only one of which develops to maturity), was considered by Sadovy & Domeier (2005) as potentially representing the ancestral sexual pattern in the Serranidae. The view that this gonochoristic arrangement preceded protogyny during the evolution of the Serranidae differs, however, from that drawn by Erisman & Hastings (2011) on the basis of the cladogram they derived from the morphological and molecular data for those species of the Anthiinae and Serraninae for which the sexual pattern was known. From this cladogram, the authors concluded that the members of the Anthiinae had retained protogynous hermaphroditism, as did certain genera of the serranines, while gonochorism evolved in the *Paralabrax* genus. The

gonochorist *E. armatus*, however, was not included by Erisman & Hastings (2011) in their cladistic analysis because the requisite taxonomic data for this anthiine were not available. The question is therefore raised as to whether harlequin fish *Othos dentex* (Cuvier 1828), which co-occurs with *E. armatus* in south-western Australian waters, is likewise a gonochorist and does not possess characteristics indicative of the possession of a juvenile bisexual phase, or whether it is a protogynous hermaphrodite, as is typically the case with anthiines (Erisman & Hastings, 2011).

In the context of reproductive biology, it is noteworthy that certain serranids and members of the related epinephelids exhibit marked sexual dichromatism, with the colours or markings of the males being particularly pronounced (Shapiro, 1981; Colin *et al.*, 1987; Colin, 1992, 1994; Crabtree & Bullock, 1998; Erisman & Allen, 2005). While such dichromatism is restricted to the spawning period in some species, it is permanent in others (Lavenda, 1949; Shapiro, 1981; Hastings & Petersen, 1986; Kodric-Brown, 1998). The development of such nuptial colouration in fishes plays a role in agonistic interactions among males and during their courtship of females (Kodric-Brown, 1998).

The colour pattern of *O. dentex*, an anthiine endemic to the temperate waters of southern Australia, where it occurs around shallow rocky reefs and in caves (Gomon *et al.*, 2008), varies markedly. While this variation includes large blotches that range from yellow to green and the presence of bright blue spots in some individuals (Gomon *et al.*, 2008), it is not known whether such variations are related to the sex of the individual and the attainment of maturity.

Othos dentex co-occurs over reefs on the cool south coast of Western Australia with the protogynous hermaphroditic labrids western blue groper *Achoerodus gouldii* (Richardson 1843) and foxfish *Bodianus frenchii* (Klunzinger 1879), and the gonochoristic sea sweep *Scorpis aequipinnis* Richardson 1848, which are all fished recreationally and commercially. Each of these species is long-lived, with maximum ages ranging from 68 to 78 years (Coulson *et al.*, 2009, 2012; Cossington *et al.*, 2010). A preliminary study involving counts of opaque zones in otoliths from a small sample of *O. dentex* obtained mainly from the waters of South Australia indicated that this anthiine could live for as long as 42 years (Saunders *et al.*, 2010).

On the basis of the empirical relationships derived by Froese & Binohlan (2000) from data for a wide range of fish species, the lengths (but not the ages) of both the females and males of *S. aequipinnis* at maturity were far greater than would be expected from their asymptotic lengths and maximum ages (Coulson *et al.*, 2012). There has thus apparently been strong selection pressure for *S. aequipinnis* to attain a relatively large size prior to maturity over reefs off the southern coast of Western Australia (Coulson *et al.*, 2012).

During this study, a wide size range of *O. dentex* was collected from the south coast of Western Australia in each calendar month to derive data aimed at answering the following questions regarding the reproductive biology of this species. (1) Is *O. dentex* a protogynous hermaphrodite or a gonochorist and, if it is the latter, do its testes possess an 'ovarian' lumen, as is typical of serranids, or is its centre occupied by a sperm duct, as with the co-occurring and likewise anthiine *E. armatus*? (2) How do the sexual patterns and gonadal characteristics of *O. dentex* equate with proposed theories regarding the evolution of gonochorism and hermaphroditism in serranids? (3) Are the different colours of the spots on the ventral body surface of *O. dentex* related to the sex of the individual and, if so, does their intensity increase

quantitatively during the spawning period? (4) In view of the trends exhibited by *S. aequipinnis*, are the lengths and ages at maturity of the co-occurring *O. dentex* consistent with those that would be expected from the respective maximum ages and associated adult mortality and the asymptotic lengths derived from the growth curves for this species?

MATERIALS AND METHODS

SAMPLING AND LENGTH AND MASS MEASUREMENTS

Othos dentex were obtained monthly or bimonthly between March 2010 and November 2011. These fish came from around reefs along the coast and around islands from numerous locations in waters between Albany (35° 01′ S; 117° 58′ E) and Esperance (33° 45′ S; 21° 55′ E) on the south coast of Western Australia. The majority (86%) of the 380 *O. dentex* caught were obtained by spear fishing when either snorkelling or scuba diving around reefs in water depths up to 30 m between 0800 and 1400 hours. The remaining 52 fish were obtained from the catches of recreational and commercial fishers. Although gonads were provided with the latter fish and could be staged macroscopically, accurate masses could only be recorded for the gonads of six of these individuals because of the damage caused during filleting. The spear fishing was undertaken by researchers experienced in this technique, and because this species does not school and is relatively sedentary, most of the individuals sighted were caught.

The total length (L_T) of each *O. dentex* was recorded to the nearest 1 mm and the total wet mass (M) of each intact individual fish and the wet mass of each intact gonad (M_G) were recorded to the nearest 0·1 and 0·01 g, respectively. Analysis of covariance (ANCOVA) was employed to determine whether the mass and length relationships for females and males differed and therefore whether it was appropriate to derive a single relationship for the two sexes. For this analysis, M was employed as the dependent variable, L_T as the independent variable and sex as the fixed factor.

AGE AND GROWTH

When intact, the sagittal otoliths of each *O. dentex*, which are particularly fine and fragile, were removed, cleaned in fresh water and stored dry. The otoliths of 84 individuals (22%) were damaged by spear fishing or when recreational and commercial fishers were using the iki-jimi method to kill these fish (www.ikijime.com), and could not be used for ageing. When intact, one otolith from each individual was embedded in clear epoxy resin and cut transversely through its primordium into *c*. 300 μm thick sections using an Isomet low-speed diamond saw (www.buehler.com/equipment/sectioning-equipment/precision-diamond-wafering-saws/isomet-low-speed-saw). Sections were polished with fine, wet and dry sand paper (1200 grade) and mounted on microscope slides using DePX mounting adhesive (http://biophoretics.com/biochemicals-a-z/755-depex-mounting-medium-for-histology-serva.html) and a cover slip. A digital microscopic image of each sectioned otolith, and of its peripheral region at a higher magnification, was used for counting opaque zones and measuring the distances required for marginal increment analysis. These images were taken using transmitted light and by employing an Olympus DP70 camera mounted on an Olympus BX51 compound microscope (www.olympus.com). All images were archived in Adobe Photoshop CS5 (www.adobe.com), which enabled the opaque zones to be readily counted and the distances used for marginal increment analysis to be measured accurately. All counts and measurements were made on the dorsal side of the otolith.

The trends exhibited throughout the year by the mean monthly marginal increments on otoliths were examined to confirm that a single opaque zone is typically formed annually in the otoliths of *O. dentex*. The marginal increment, *i.e.* the distance between the edge of the outermost opaque zone and the periphery of the otolith, was expressed as a proportion of the distance between the edge of the second outermost opaque zone and the periphery of the

otolith, noting that all otoliths had at least two opaque zones, reflecting the fact that no fish of <183 mm L_T were caught. All distances were measured to the nearest 0·01 mm along the axis perpendicular to the opaque zones and on the dorsal side of the otolith adjacent to the sulcus.

The opaque zones in each sectioned otolith of *O. dentex* were counted independently by two readers and the findings of the more experienced reader were used for subsequent analyses. The level of precision between the counts of opaque zones recorded by the two readers for all otoliths was assessed using the coefficient of variation (c.v.) of Chang (1982). The resultant c.v. value of 1·9% is well below the 5% considered acceptable by Campana (2001), demonstrating that there was a high level of agreement between the counts of the two readers for this relatively long-lived species.

Each *O. dentex* was assigned an age, based on the number of opaque zones in its otolith, its date of capture, the average birth date (approximate mid-point of the spawning period) of 1 December for *O. dentex* and the mean time of year when the outer opaque zone becomes delineated at the periphery of the otoliths (1 December).

A separate growth curve was fitted to the L_T (mm) at age t (years) of the females and males of *O. dentex* using the von Bertalanffy growth equation, *i.e.* $L_T = L_\infty \left[1 - e^{-k(t-t_0)}\right]$, where L_∞ is the asymptotic length (mm) predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length. The curves were fitted by employing Solver in Microsoft Excel to minimize the sum of squared residuals between the observed and expected lengths at age (x), thus maximizing the log-likelihood, λ, for each curve. Ignoring the constants, λ was calculated as $\lambda = -\frac{1}{2}n \ln(xn^{-1})$, where $n =$ sample size. The 95% c.l. for the von Bertalanffy growth parameters was calculated by re-sampling the length-at-age data, with replacement, to produce 1000 data sets and fitting the growth equation to each data set. The point estimates and associated 95% c.l. for the growth parameters were taken as the median, 2·5 and 97·5 percentile values, of the resultant 1000 estimates for each growth parameter from this re-sampling analysis.

A likelihood-ratio test (Cerrato, 1990) was used to determine whether the growth curves of the two sexes were significantly different. The test statistic was determined as twice the difference between the log likelihoods obtained by fitting a common growth curve to the data for the two sexes combined and by fitting separate growth curves to the data for each sex. The hypothesis that the growth of the two sexes could be appropriately described by a single growth curve was rejected at the $\alpha = 0.05$ level of significance if the above test statistic exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two approaches, *i.e.* 3 (Cerrato, 1990).

Values of total mortality (Z) for each sex were estimated from the age composition of fully recruited fish using the equation of Chapman & Robson (1960), *i.e.* $Z = \ln\left[1 + \overline{X} - n^{-1}\right] - \ln\overline{X} - \left\{(n-1)(n-2)\left[n(T+1)(n+T-1)\right]^{-1}\right\}$, where $\overline{X}$ is the mean of the integer ages of fully recruited fish relative to the age at full recruitment, n is the number of such fish and $T = n\overline{X}$. The age at full recruitment of each sex was taken as 1 year older than the peak in the age-frequency distribution for the respective sex. The 95% c.l. for Z were estimated as the 2·5 and 97·5 percentiles of 10 000 estimates of Z obtained by re-sampling the age compositions, with replacement. Catch curve analysis was restricted to fish collected by spear fishing by researchers. As the vast majority of fish sighted were caught, these samples are considered representative of the size and age compositions of the medium-sized and large fish within the population in this region. Hoenig's (1983) equation, $\ln Z = 1.46 - 1.01 \ln A_{max}$, was also employed to estimate Z for each sex, where A_{max} is the maximum age of the respective sex, noting that such estimates of Z are frequently used as estimates of natural mortality.

REPRODUCTION

The gonado-somatic index (I_G) for each female and male *O. dentex*, with an $L_T \geq$ the respective L_{T50} for that sex at maturity, was calculated as $I_G = 100 \, M_G \, M^{-1}$, where M_G = wet mass of gonad and $M =$ total wet mass of fish. The criteria for the gonadal stages were taken largely from those developed for the morphologically similar gonads of another

TABLE I. Macroscopic and histological characteristics of the stages in the development of the ovaries of *Othos dentex*

Stage	Macroscopic characteristics	Histological characteristics
I–II, Immature–resting	Small, pale pink, transparent. Oocytes not visible.	Chromatin nucleolar oocytes dominate, perinucleolar oocytes sometimes present.
III, Developing	Larger than previous stages, oocytes become visible.	Chromatin nucleolar, perinucleolar and cortical alveolar oocytes present. Occasional yolk granule oocytes present.
IV, Maturing	Larger still, pale orange–yellow yolk granule oocytes present and visible through ovarian wall.	Abundant cortical alveolar and yolk granule oocytes.
V, Pre-spawning	Larger than previous stages, occupying half the body cavity. Blood vessels clearly visible.	Yolk granule oocytes dominate. Tightly packed.
VI, Spawning	Hydrated oocytes visible through ovarian wall. Paler than previous stage. Blood vessels prominent.	Some yolk granule oocytes, numerous hydrated oocytes and migratory nucleus stage oocytes or post-ovulatory follicles.
VII, Spent	Smaller than previous stage, pinker in colour. Flaccid.	Remaining yolk granule oocytes undergoing atresia.
VIII, Recovering	Smaller, dark pink. Oocytes not visible. Flaccid.	Connective tissue present. Chromatin nucleolar oocytes present.

serranid, *E. armatus*, from the same region (Moore *et al.*, 2007) and which had been adapted from studies by Laevastu (1965) and Rhodes & Sadovy (2002). Ovarian stages V and VI were separated, however, in this study. The details given in the study by Wallace & Selman (1981) were used to identify the various oocyte stages. The prevalence of the different gonadal stages in females and males with an $L_T \geq$ their respective L_{T50} were used, in conjunction with the I_G, to determine the duration of the spawning period, placing particular emphasis on the months when hydrated oocytes were present in ovaries (ovarian stage VI) and spermatozoa were prevalent in testes (stage IV testis). Details of the macroscopic and histological characteristics of the stages in the development of the ovaries in *O. dentex* are given in Table I.

Up to 10–20 gonads from individuals of each sex in each calendar month and covering a wide size range of fish were placed in Bouin's fixative for 24 h and then dehydrated in a series of increasing concentrations of ethanol. The mid-regions of these gonads were then embedded in paraffin wax, cut into 6 µm transverse sections and stained with haematoxylin and eosin. The gonadal sections were examined using a compound microscope to determine their histological characteristics at key stages in development. In addition, the gonads of 38 individuals, covering the full size range of fish caught and thus including juveniles, were sectioned at intervals along their entire length. The sections from the mid region of each gonad of these fish were broadly typical of that gonad as a whole.

The L_T at which 50% (L_{T50}) and 95% (L_{T95}) of females and males become mature during the spawning period were estimated by logistic regression analysis. For this analysis, fish with gonads at stages III and above were considered mature. Stage III was chosen as the minimum stage because the trends exhibited by the prevalence of

each gonad stage over time indicated that, if a gonad had reached stage III during the spawning period, it was destined to become mature later in that period. The logistic equation used to relate the probability (ρ) that a female, or male, is mature to L_T (mm) was $\rho = \left\{ 1 + e^{\left[-\ln(19)(L_T - L_{T50})(L_{T95} - L_{T50})^{-1} \right]} \right\}^{-1}$. Logistic curves were fitted employing Solver in Microsoft Excel by maximizing the log-likelihood, λ, which was calculated as $\lambda = \sum_j \left\{ X_j \ln \rho_j + (1 - X_j) \ln (1 - \rho_j) \right\}$, where the jth fish was represented by $X = 0$ if it was immature and $X = 1$ if it was mature. The data were randomly re-sampled, with replacement, and analysed to create 1000 estimates of the parameters of the logistic equation and of the probability of females and males being mature at each value in a range of specified L_T. The point estimate and lower and upper 95% C.L. for the logistic parameter and probability of maturity at each length were taken as the median, 2·5 and 97·5 percentiles, of the 1000 estimates for each parameter and the probability of maturity at the estimated length. The same form of regression analysis was used to determine the ages at which 50% (A_{50}) and 95% (A_{95}) of females and males reach sexual maturity, together with their 95% C.L.

Histological sections of stage V ovaries from two mature female *O. dentex* caught during the peak of the spawning period were used to assess whether *O. dentex* has determinate or indeterminate fecundity (Hunter *et al.*, 1985; Hesp *et al.*, 2004; Cossington *et al.*, 2010). This was undertaken by examining the distributions of the diameters of 200 oocytes for each fish that had been determined from the circumferences of those oocytes, which had been measured to the nearest 0·1 μm in histological sections using the computer imaging package Leica IM 1000 (Leica Microsystems; www.leica-microsystems.com). Measurements were restricted to those oocytes in which the nucleus was clearly visible to ensure that the oocyte had been sectioned through its centre. The stage in development of each oocyte used for these measurements was recorded.

The empirical equations developed by Froese & Binohlan (2000) for relationships between life-history characteristics from data for a wide range of species are as follows: females $\log L_{T50} = 0.9469 \log L_\infty - 0.1162$ s.e. $= 0.122$, males $\log L_{T50} = 0.8915 \log L_\infty - 0.1032$ s.e. $= 0.147$ and pooled sexes $\log A_{max} = 0.5496 + 0.9570 \log A_{50}$ s.e. $= 0.194$. Estimates were obtained from the EXCEL workbook, popdynJFB.zip, developed by Froese & Binohlan (2000). Logarithms are expressed as $\log_{10}$. More recently, Jarić & Gačić (2012) developed the following relationship between the maximum age and the age at maturity to accommodate long-lived species, $A_{max} = \{4 \cdot 31[1 \cdot 52 \, A_{50}^{-0.72} - 0 \cdot 16]^{-1}\}^{0.99}$. These equations were used to determine whether the values for these variables for *O. dentex* are typical of those of most teleosts or parallel, for example, those for *S. aequipinnis* on the same coast (Coulson *et al.*, 2012).

DICHROMATISM

A preliminary investigation demonstrated that the spots on the lower half of the body and posterior to the pectoral fin of *O. dentex* vary from bright yellow through green to bright blue. All fish caught during the bimonthly or monthly spear fishing trips conducted between September 2010 and November 2011 were photographed. This thereby provided images showing the colouration of the spots on the body of fish for all calendar months between September and February and thus encompassing all but the last month of the protracted spawning period of this species. These fish had been placed on ice soon after capture and were photographed within 4–6 h of capture using a Nikon D60 digital single-lens reflex camera. Employing Photoshop CS5, the colour ratio (C_R), representing the average percentage contributions of the colours cyan (blue) to yellow in a 50×50 pixel square in the centre of the three largest spots below the dorsal fin, was determined using the following equation: $C_R = C_R = \overline{c} \, \overline{y}^{-1}$, where $\overline{c}$ and $\overline{y}$ are the average percentage contributions of cyan (blue) and yellow. When the C_R values are $\leq c$. 0·5, the spots are yellow, whereas when they are $\geq 0 \cdot 8$ the spots are a bright blue and those with intermediate values are green. While fish tend to become darker between the time of capture and photography, the ratio of the numbers of yellow to blue pixels in a spot did not change with time.
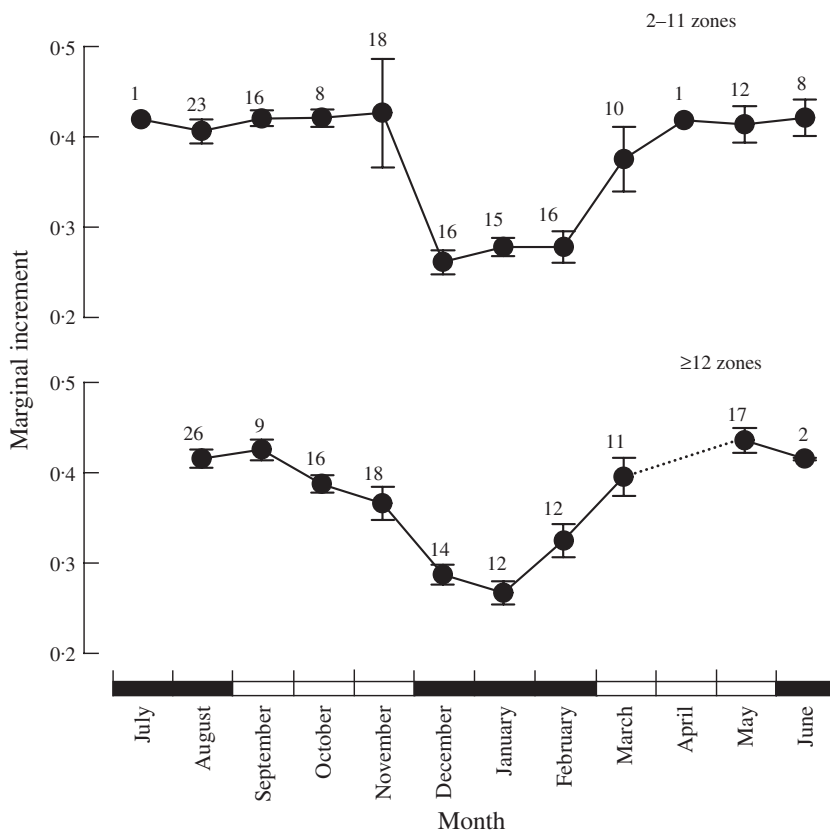
FIG. 1. Mean ± s.e. monthly marginal increments on the otoliths of *Othos dentex* with two to 11 opaque zones and ≥12 opaque zones. Sample sizes are shown above the mean values.

RESULTS

VALIDATION OF AGEING PROCEDURE

Alternating opaque and translucent zones were clearly visible in sectioned otoliths of *O. dentex*. The mean marginal increment for otoliths with two to 11 zones remained >0·40 between August and November and then declined to a minimum of 0·26 in December, before subsequently increasing to elevated levels in June, which were very similar to those from August to November (Fig. 1). The trends exhibited throughout the year by the mean monthly marginal increment for otoliths with ≥12 zones essentially parallel those just described for otoliths with two to 11 opaque zones (Fig. 1).

The single pronounced decline and the following progressive increase during the year by the mean monthly marginal increments for otoliths with different numbers of opaque zones demonstrates that, irrespective of the number of opaque zones, a single new opaque zone is typically formed annually in the otoliths of *O. dentex*. The number of opaque zones in otoliths can thus be used to determine the age of the individuals of this species.

LENGTH AND AGE COMPOSITIONS AND GROWTH

ANCOVA showed that the relationships between M and L_T for intact females and males of *O. dentex* were not significantly different ($P > 0.05$) and thus the data for these variables for the individuals of both sexes were pooled. The equation for the linear relationship between the ln of M and L_T of both sexes combined is $\ln M = 3.125(\ln L_T) - 11.954$ ($r^2 = 0.98$, mean square $= 0.007$, $P < 0.05$, $n = 380$). This relationship between the M and L_T of intact fish was then used to estimate the mass of each *O. dentex* that had been filleted.

The *O. dentex* that were sampled ranged from 183 to 605 mm in L_T and their ages ranged from 2 to 37 years (Fig. 2). The females and males ranged in L_T from 250 to 605 mm and 183 to 570 mm, and in age from 2 to 37 years and 3 to 31 years, respectively.

The L_T of the vast majority of both females (88%) and males (90%) was between 325 and 554 mm and those of both sexes produced an ill-defined modal L_T class at 450–474 mm (Fig. 2). Both sexes were represented in each 5 year age class interval up to 30–34.9 years (Fig. 2).

The r^2 values for the von Bertalanffy growth curves fitted to the lengths at ages of females and males [Fig. 3(a), (b)] were relatively high (Table II). Although the curves for the two sexes were significantly different ($P < 0.001$), the difference between the predicted L_T at age was <5% for all ages up to 27 years [Fig. 3(c)], which encompassed the ages of the majority of fish. As the growth curves of female and male *O. dentex* were similar throughout the majority of their life spans, a common von Bertalanffy growth curve was fitted to the lengths at age of both sexes [Fig. 3(d)]. The highly negative t_0 values for both sexes reflect the fact that, despite a very concerted sampling effort, the samples did not contain the youngest (and smallest) fish. While the growth curves thus adequately describe the lengths at ages within the observed range of ages of females and males, they do not describe growth during the early life of the two sexes of *O. dentex*.

The age at full recruitment for both the female and male *O. dentex* was 13 years. The respective estimates of Z derived for the females and males of this species using the equations of Chapman & Robson (1960) were similar, *i.e.* 0.166 year^{-1} (95% c.i. $= 0.136-0.210$) and 0.153 year^{-1} (95% c.i. $= 0.119-0.208$). These estimates of Z were only slightly greater than those derived for the corresponding sexes using Hoenig's (1983) equation, *i.e.* 0.134 and 0.112 year^{-1}.

REPRODUCTION

The mean monthly I_G for females $\geq$ the L_{T50} (345 mm) rose sharply from 0.9 in August to 3.4 in September and then to a maximum of 4.2 in November and December, after which it declined over the ensuing months to their minimal levels in May and June (Fig. 4). While the mean monthly I_G for males $\geq$ the L_{T50} (356 mm) in each month was far lower than those for females, they followed a very similar trend, increasing sharply in September and remaining elevated through to December, and then declining sequentially (Fig. 4).

Stage I ovaries contain only ovarian tissue and their germ cells comprise numerous previtellogenic oocytes [Fig. 5(a)], while stage I testes contain the occasional spermatocyst with spermatogonia [Fig. 5(b)]. Stage V ovaries are characterized by possessing large numbers of yolk granule oocytes [Fig. 5(c)], while stage VI ovaries also
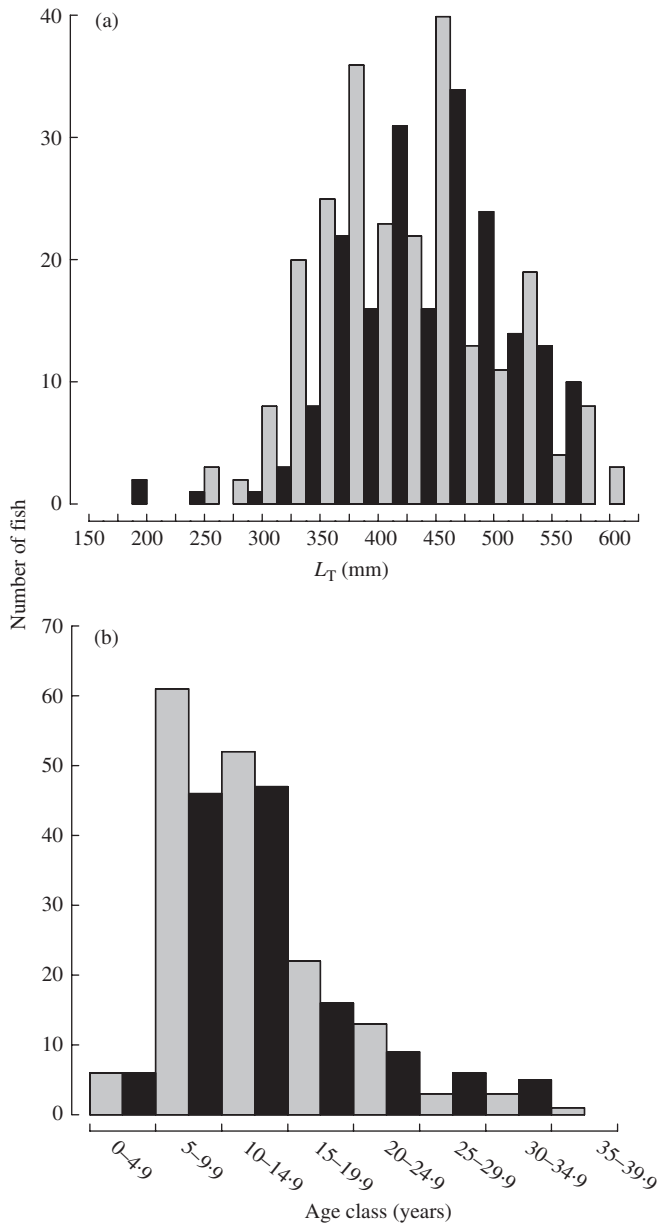
FIG. 2. (a) Total length frequency (L_T) of female (▨; $n = 237$) and male (■; $n = 195$) and (b) age-frequency distributions of female (▫; $n = 161$) and male (■; $n = 135$) *Othos dentex*.

contain numerous hydrated oocytes [Fig. 5(d)] and migratory nucleus-stage oocytes or post-ovulatory follicles. The germ cells in the spermatocysts of stage III testes range from spermatogonia to spermatocytes, with those of advanced stage III testes occasionally containing spermatozoa [Fig. 5(e)]. The prominent central sperm duct that characterizes the testes of adult *O. dentex* is clearly seen in the low magnification
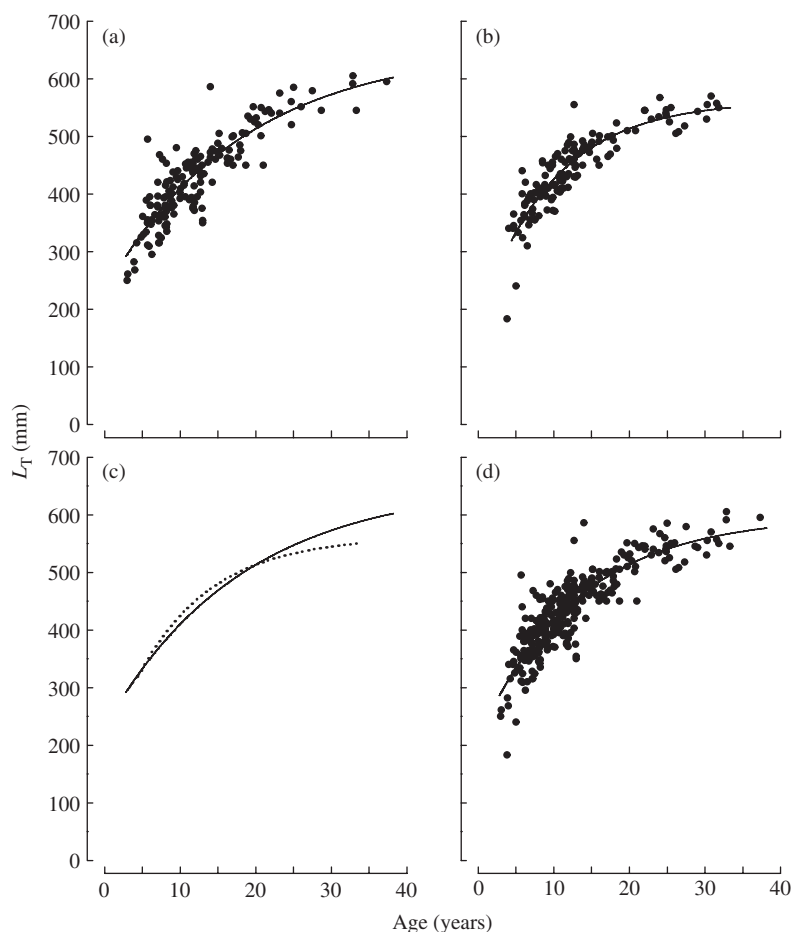
FIG. 3. von Bertalanffy growth curves for *Othos dentex*, fitted to the total lengths (L_T) at age of (a) females
($n = 161$), (b) males ($n = 135$) and (d) both sexes combined ($n = 296$). (c) The separate curves for
each sex (——, females; ...., males) are indicated.

micrograph of the stage IV testis shown in Fig. 5(f). The sperm duct is surrounded
by spermatocysts, within which the germ cells increase in maturity from those at the
periphery to those at the centre of the testis. Sperm sinuses are present neither in the
periphery of the testis shown in Fig. 5(f) nor in any other testis of *O. dentex*.

In August, the ovaries were predominantly at stage III (developing) and none was
beyond stage IV (maturing) (Fig. 6). By September and October, the most common
ovarian stage was V (pre-spawning) with a few at stage VI (spawning). Fish with
stage VI ovaries were subsequently present between November and March. Most
ovaries were at stage VII (spent) during February and March and, by May, the vast
majority were at stages VII or VIII (recovering spent) (Fig. 6). The prevalence of
the various stages in the development of the testes of males in sequential months
followed a trend similar to that described for ovaries, with many males possessing
stage IV (mature and ripe) testes between September and February (Fig. 6). The

TABLE II. The von Bertalanffy growth equation parameters L_∞, k and t_0, derived from the total lengths at age of females and males of *Othos dentex*, and of both sexes combined, together with their lower and upper 95% C.L.

	von Bertalanffy growth parameters				
	L_∞ (mm)	k (year^{-1})	t_0 (years)	r^2	n
Female					
Estimate	654	0·05	−7·92	0·77	161
Lower	572	0·03	−11·60		
Upper	736	0·08	−4·24		
Male					
Estimate	562	0·10	−3·73	0·80	135
Lower	535	0·07	−5·83		
Upper	589	0·13	−1·64		
Sexes combined					
Estimate	598	0·08	−5·77	0·77	296
Lower	564	0·06	−7·82		
Upper	631	0·09	−3·72		

n = sample size.

above trends in the mean monthly I_G indices and the prevalence of the various stages in the development of, particularly, the ovaries demonstrate that *O. dentex* spawns from September to March.

The distributions of oocyte diameters in sections from two stage V (pre-spawning) females collected from the spawning period were continuous. The modal oocyte diameter of 25–49 µm represents chromatin nucleolar and perinucleolar oocytes, while the diameters of the cortical alveolar and yolk granule oocytes ranged from 75 to 174 and 150 to 424 µm. This pattern of distribution of multiple oocyte stages within mature ovaries implies that *O. dentex* has indeterminate fecundity and exhibits multiple batch spawning (Hunter *et al.*, 1985).

During the spawning period, the smallest female and male with mature gonads were 310 and 333 mm L_T, respectively. The per cent of mature females increased sharply from 13% in the 300–324 mm class to over 90% for all fish ranging from 375 to 424 mm L_T and then increased to 100% for all fish $\geq$ 425 mm L_T [Fig. 7(a)]. Likewise, the per cent of mature males increased from 30% in the 325–349 mm class to 95% in the 400–424 mm class, with all males $\geq$ 425 mm L_T possessing mature gonads [Fig. 7(b)]. The values for L_{T50} of females and males were 345 and 356 mm, respectively (Table III).

The youngest mature female and male were both 4 years old. The percentage frequency of mature females during the spawning period increased from 50% of fish in the 4–5·9 age class to 58% in fish in the 6–7·9 age class, with all fish $\geq$10 years old being mature [Fig. 7(a)]. The trends exhibited by males were similar, with 14% of the 4–5·9 age class and all fish of 10 years and older being mature [Fig 7(b)]. The A_{50} for both males and females was 6·3 years (Table III).

The L_{T50}, for the females and males of *O. dentex*, fell within the range of expected values derived from the equations of Froese & Binohlan (2000) (Table IV). In contrast, the maximum observed ages of the two sexes far exceeded the corresponding point estimates derived from the equation of Froese & Binohlan (2000) and, while
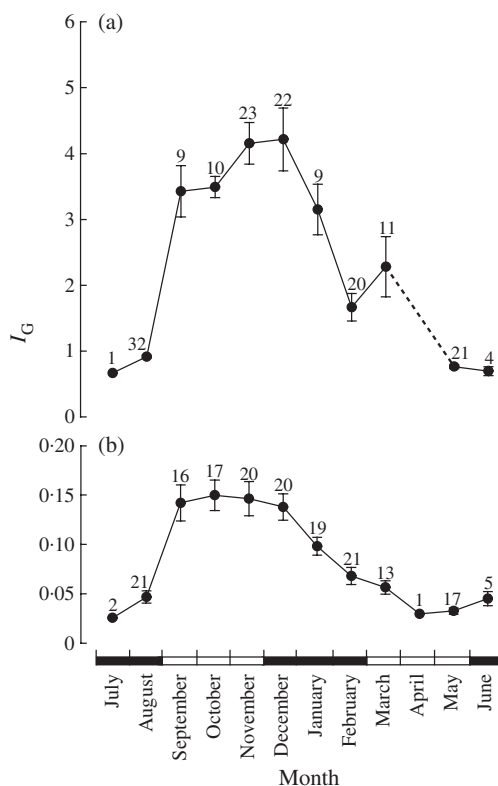
FIG. 4. Mean ± S.E. monthly gonado-somatic indices (I_G) for (a) female and (b) male *Othos dentex* with total
lengths (L_T) ≥ their respective L_T at 50% maturity (L_{T50}). Sample sizes are shown above the mean values.

the estimate for males lay just within the upper end of the range of expected values,
that for females lay well outside that range. Furthermore, when using the equation of
Jarić & Gačić (2012), the maximum observed ages of the two sexes exceeded, to an
even greater extent, the predicted maximum ages derived from the A_{50} at maturity
(Table IV).

DICHROMATISM

The body surfaces of all juveniles and adult females of *O. dentex* contain longi-
tudinal blue flecks on the dorsal surface and very large yellow spots on the lower
half of the body, posterior to the pectoral fin [Fig. 8(a)–(c)]. In contrast, as males
become mature, the spots change from yellow to green and, as shown in Fig. 8(d),
finally to blue, with the blue flecks on the dorsal surface of the body particularly
becoming more prominent.

The mean C_R values for the above spots in females and males up to 325–349 mm
L_T were similar, ranging only from 0·35–0·45 (Fig. 9), which corresponds to a yellow
colouration. The C_R value remained similar for females as this sex increased to its
maximum size, demonstrating that the spots retained the same yellow colour through-
out life. In contrast, the C_R value increased markedly in the 350–374 mm class of
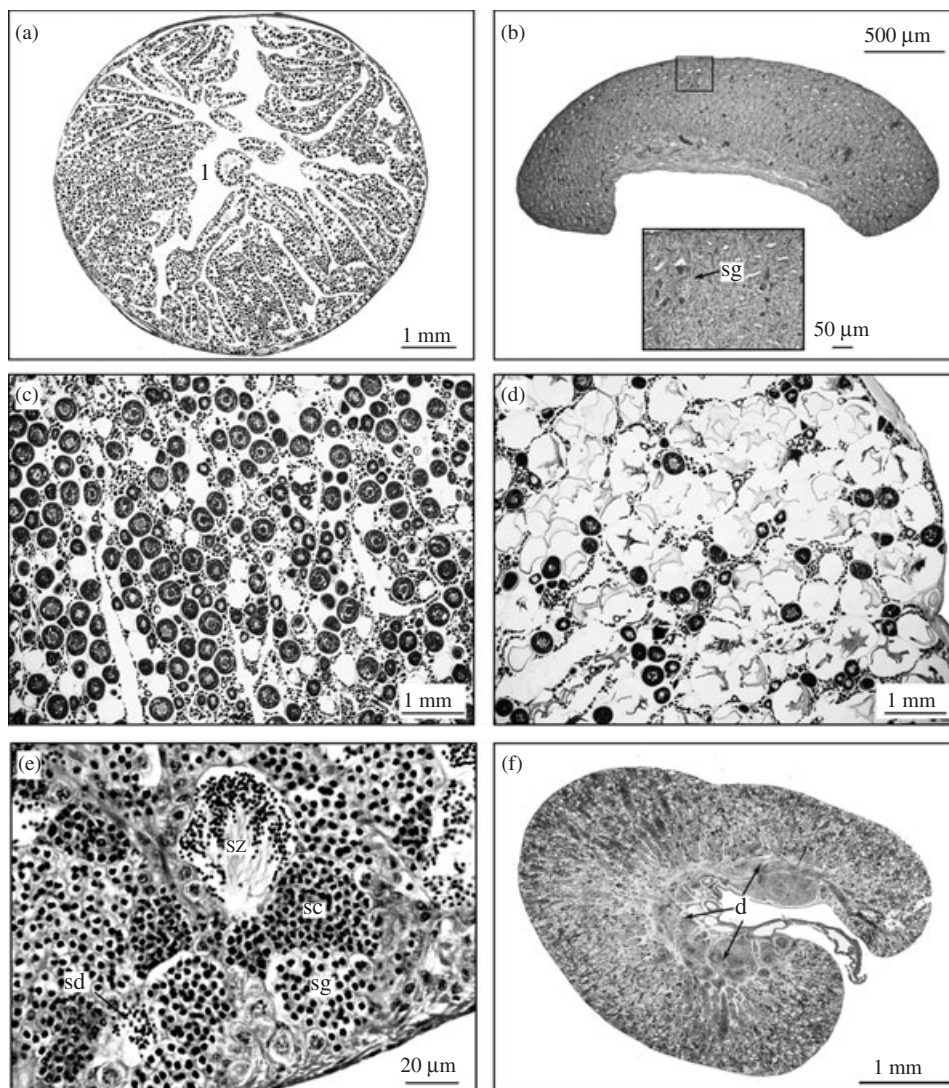
FIG. 5. Histological sections of gonads of *Othos dentex* caught during the spawning period. (a) Stage I ovary of a female of 292 mm total length (L_T), (b) stage I testis of a male of 280 mm L_T, with inset showing spermatogonia in one of the spermatocysts, (c) stage V (pre-spawning) ovary of a female of 400 mm L_T containing large numbers of yolk granule oocytes, (d) stage VI (spawning) ovary of a female of 406 mm L_T containing numerous hydrated oocytes, (e) high magnification of a region of a stage III testis of a male of 340 mm L_T and (f) stage IV (spawning) testes of a male of 490 mm L_T. l, lumen; d, sperm duct; sg, spermatogonia; sc, spermatocyte; sd, spermatid; sz, spermatozoa.

males and continued to rise with further increases in L_T, reflecting a progressive change from yellow through green to blue (Fig. 9).

During the spawning period, the mean C_R value of males increased sharply from 0·80 in September to 1·03 in November and December and then declined to 0·87 in February reflecting changes in the intensity of the blue colour (Fig. 9).
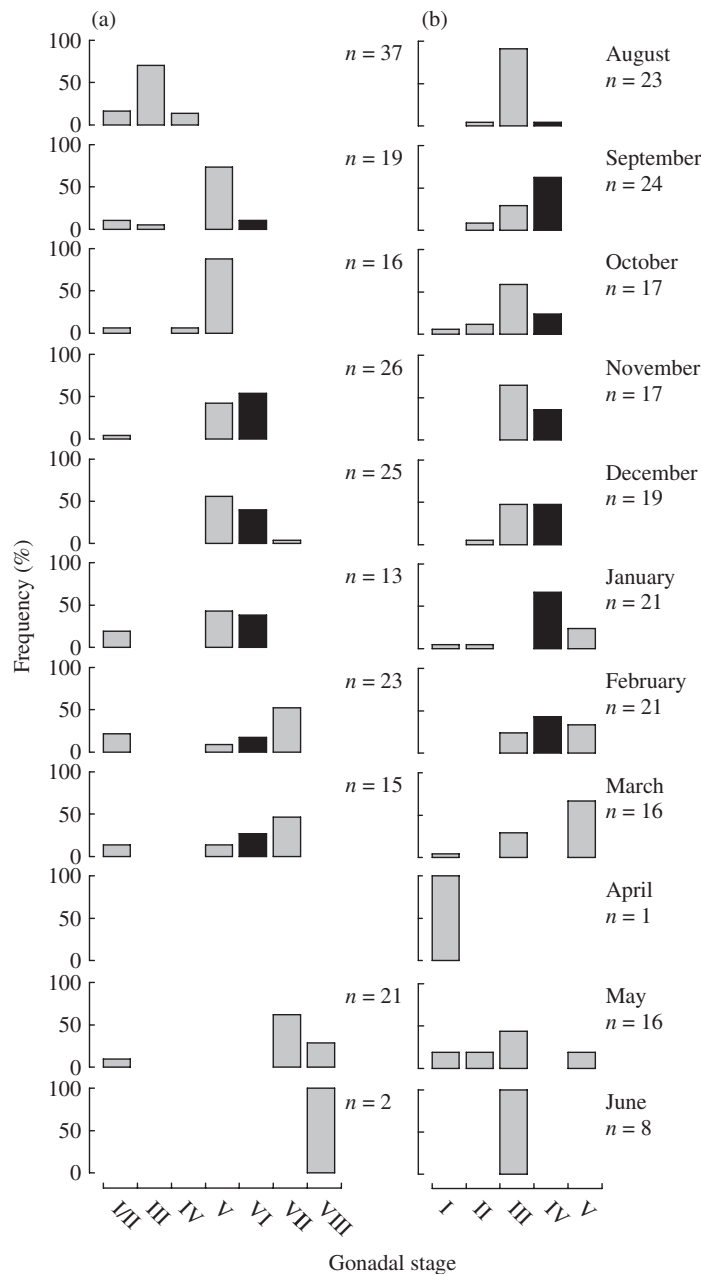
FIG. 6. Monthly percentage frequencies of occurrence of sequential stages in the gonadal development (□) of (a) females and (b) males of *Othos dentex* ≥ their total length (L_T) at 50% maturity (L_{T50}), *i.e.* 345 and 356 mm. Histograms for stage VI (spawning) ovaries and stage IV (spawning) testes are highlighted (■). n = sample size.
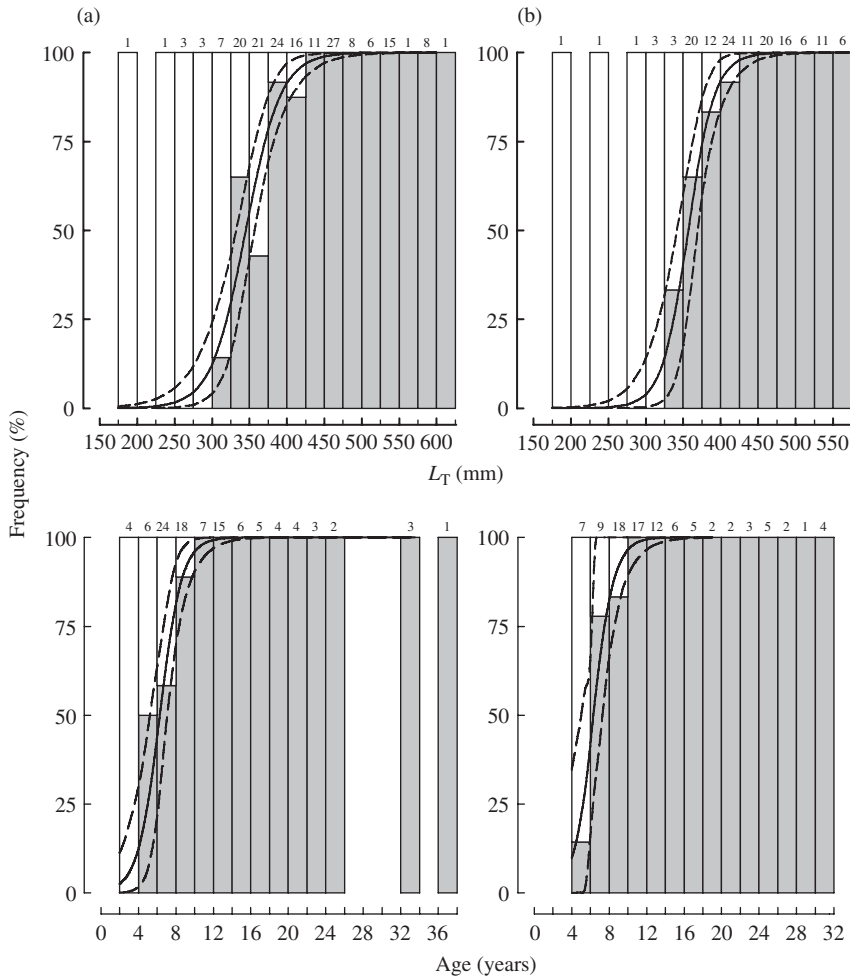
FIG. 7. Percentage frequencies of occurrence of (a) female and (b) male *Othos dentex*, during their spawning period, *i.e.* September to March, with immature (stages I and II; □) and mature (stages > II; ▣) gonads in sequential 25 mm total length (L_T) classes and sequential 2 year age classes. Logistic curves (——) and their associated 95% C.L. (........) were derived from the probability that a fish at a given L_T or age is mature. Sample sizes are shown.

DISCUSSION

SEXUAL PATTERN

The following results demonstrate that *O. dentex* is a gonochorist. (1) Length-frequency distributions for the females and males, which are based on data collected from many locations and different times of the year, exhibited no evidence of a marked overall bimodality that could be attributed to differences between the lengths of the two sexes. (2) As with length, the age-frequency distributions showed no underlying evidence of a sex-based bimodality. Indeed, apart from the oldest female, both sexes were represented in each age class, and the same two age classes, *i.e.*

TABLE III. Estimates, and their associated 95% C.L., for the total lengths (L_T) and ages (A) at which 50 and 95% of the females and males of *Othos dentex* reach maturity, *i.e.* L_{T50} and L_{T95}, and A_{50} and A_{95}

	L_{T50} (mm)	L_{T95} (mm)	A_{50} (years)	A_{95} (years)
Female				
Estimate	345	412	6·3	9·7
Lower	333	391	5·2	8·3
Upper	357	433	7·1	11·2
Male				
Estimate	356	408	6·3	9·6
Lower	341	388	5·0	6·5
Upper	369	428	7·3	11·3

5–9·9 and 10–14·9 years, were sequentially by far the most abundant in both sexes. (3) Histological examination of a large number of gonads from a wide length and age range of fish from different times of the year, representing individuals of both juveniles and adults and all stages in gonadal development, demonstrated that the gonads of each fish contained solely ovarian tissue or testicular tissue. Thus, while the smallest fish could not be obtained and thereby enable the characteristics of the gonads to be determined very early in life, the above findings satisfy the criteria of Sadovy & Shapiro (1987) for elucidating whether a species is an hermaphrodite or a gonochorist (Sadovy & Domeier, 2005; Sadovy de Mitcheson & Liu, 2008).

The demonstration that *O. dentex* is a gonochorist parallels the finding of Moore *et al.* (2007) for *E. armatus*, another anthiine. While a third athiine, New Zealand orange perch *Lepidoperca aurantia* Roberts 1989, was recorded by Roberts (1989) as probably a gonochorist in his taxonomic review of a group of serranids in New

TABLE IV. The total length at which 50% are mature (L_{T50}) and maximum age (A_{max}) determined for *Othos dentex* during this study, and estimates of the expected values for the life-history characteristics of *O. dentex* and their S.E. ranges, derived from the empirical relationships of Froese & Binohlan (2000) and Jarić & Gačić (2012)

	L_{T50} and A_{max} (this study)	L_{T50} from L_∞ and A_{max} from A_{50} (Froese & Binohlan, 2000)	
		Estimate	S.E. range
Females	345 mm	401 mm	303–531 mm
Males	356 mm	286 mm	204–402 mm
Females	37 years	20·6 years	13·2–32·3 years
Males	31 years	20·6 years	13·2–32·3 years
		A_{max} from A_{50} (Jarić & Gačić, 2012)	
		Estimate	
Females	37 years	17·2 years	
Males	31 years	17·2 years	

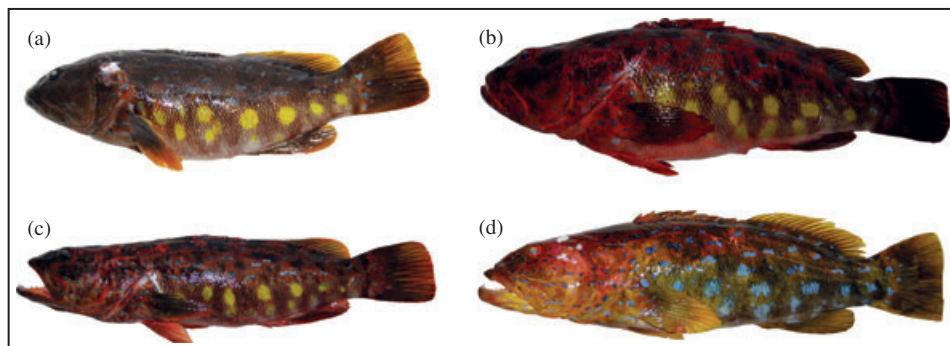L_∞, asymptotic length; A_{50}, age at which 50% are mature.

FIG. 8. Photographs showing variations in the colour of the large spots on the ventral body surface posterior to the pectoral fin of *Othos dentex*. (a) Immature female of 283 mm total length (L_T), (b) mature female of 438 mm L_T, (c) immature male of 260 mm L_T and (d) mature male of 480 mm L_T.

Zealand, this view was not based on a demonstrated detailed analysis of a wide suite of biological characteristics and thus requires verification.

The possible route taken by the evolution of gonochorism and protogyny in serranids has been considered by Sadovy & Domeier (2005) and Erisman & Hastings (2011), who drew on the pioneering work of several authors, including D'Ancona (1952), Smith (1965) and Reinboth (1970). Sadovy & Domeier (2005) stated that the central region of the testes of the adult serranids, including those of anthiines,
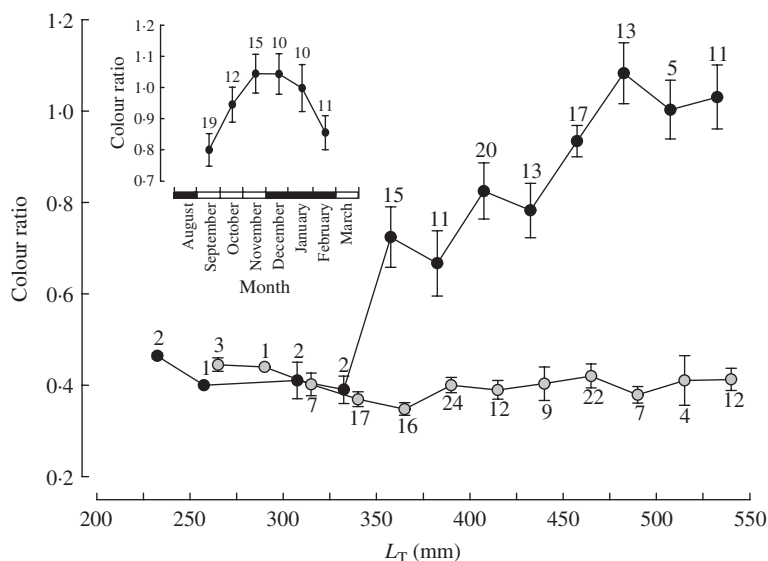

FIG. 9. Mean ± S.E. ratio of blue to yellow colouring (colour ratio) of the spots on the lower half of the body and posterior to the pectoral fin of females (○) and males (●) in sequential 25 mm total length (L_T) classes of *Othos dentex* caught throughout the year. Sample sizes for the females and males of each class are shown above or below the mean values. Inset shows the mean monthly colour ratios during the spawning period. Monthly sample sizes are shown above the mean values.

contains a central membrane-lined 'ovarian' lumen, which represents the retention of this structure from the gonads of its bisexual juvenile stage. The central location of this lumen accounts for the sperm sinuses being situated on the periphery of the testes of those species. This study has shown, however, that the central region of the testes of adults of the athiine *O. dentex* does not contain a membrane-bound 'ovarian' lumen and that this region is occupied instead by a conspicuous sperm duct. This arrangement parallels that recorded by Moore *et al.* (2007) for *E. armatus* from a different genus of the Anthiinae but found in the same geographical region as *O. dentex*. Furthermore, the gonads of all juveniles of *O. dentex* and *E. armatus* in the length and age ranges examined consisted exclusively of ovarian or testicular tissue and were thus not bisexual. While this contrasts with the situation in other gonochoristic serranids, such as *Paralabrax* species (Sadovy & Domeier, 2005), *O. dentex* and *E. armatus* might possess bisexual gonads very early in life, noting, however, that this was not the case even in individuals of the latter species whose L_T was only 60 mm and whose gonads were very undeveloped (Moore *et al.*, 2007). Thus, if bisexuality is present early in juvenile life, it disappears very early in gonadal development and long before the individuals of at least *E. armatus* reach maturity and some time before this is achieved in *O. dentex*.

Sadovy & Domeier (2005) discussed the evolution of sexual patterns in serranids based on their possession of a non-functional bisexual phase in *Paralabrax* species, in which the male and female tissues are clearly separate. The phylogenetic relationships within the Serranidae, however, have since been modified and *Paralabrax* is no longer considered the ancestral genus (Smith & Craig, 2007). Recently, Erisman & Hastings (2011) superimposed the known sexual patterns of species of anthiines and serranines on a cladogram constructed using morphological and molecular data derived for those species. The trends on the cladogram imply that protogyny was the ancestral condition in the Serranidae *sensu stricto* and was retained by members of the Anthiinae at its base, with gonochorism subsequently being evolved by the serranid genus *Paralabrax* and followed by simultaneous hermaphroditism in other members of the Serranidae.

A lack of requisite morphological and molecular data for *E. armatus* precluded the inclusion of this species by Erisman & Hastings (2011) in their cladistic analysis for the Serranidae. These authors were thus unable to apply the sexual pattern of *E. armatus*, and also that determined for *O. dentex* during this study, *i.e.* gonochorism, when using their cladogram to hypothesize the sequence of gonochorism and protogyny during the evolution of this family. Erisman & Hastings (2011) did note, however, that, as *E. armatus* and possibly *L. pulchella* were gonochorists, this sexual pattern had evolved at least once in the Anthinae. Furthermore, superimposition of sexual pattern on the species used by Erisman *et al.* (2009) for deriving a phylogenetic scheme for the Epinephelidae, a closely related family of the Serranidae, implies that gonochorism evolved on different occasions in this family.

If the scheme of Erisman & Hastings (2011) for the evolution of sexual patterns in serranids is correct, *O. dentex* and *E. armatus* presumably represent an early offshoot or offshoots within the anthiines from ancestors in which protogyny had not yet evolved or they are derivatives of species that possessed the characteristics associated with protogynous hermaphroditism (as in other anthiines), but which then became lost. It thus follows that the collection of sound relevant morphological and molecular data for *O. dentex* and *E. armatus*, which could be incorporated with those

used by Erisman & Hastings (2011), would enable a more up-to-date cladogram to be constructed for the relationships among the species of Serranidae and thus be invaluable in refining views on the evolution of sexual patterns in this family.

MAXIMUM LENGTH, LONGEVITY AND GROWTH

The maximum L_T of 605 mm recorded for *O. dentex* caught on the south coast of Western Australia during this study was similar to the corresponding value of c. 600 mm L_T recorded in a preliminary study in South Australia (Saunders *et al.*, 2010). It is thus surprising that these maximum lengths were both far less than the 750 mm standard length (= c. 860 mm L_T) recorded by Gomon *et al.* (2008) for this species in their treatise on the fishes of Southern Australia. The maximum L_T recorded for *O. dentex* in this study is still large for a species of serranid *sensu stricto*, with the above values of c. 600 mm being exceeded only by species such as barred sea bass *Paralabrax nebulifer* (Girard 1854), for which a maximum L_T of 620 mm has been recorded (Love *et al.*, 1996).

The use of marginal increment analysis demonstrated that the number of opaque zones in the otoliths of *O. dentex* could be used to determine the ages of the individuals of this species. Thus, the maximum age of 42 years recorded for *O. dentex* in South Australian waters (Saunders *et al.*, 2010), as well as the 37 years recorded in this study for populations on the south coast of Western Australia, demonstrate that this species is long-lived. These two similar values are the greatest yet recorded for a serranid *sensu stricto*, most of which are serranines (Table V). The maximum age for the Western Australian population of *O. dentex* provides another example of a reef-dwelling species from the south coast of this part of Australia having considerable longevity but it is not as great as the 68, 70 and 78 years recorded for *S. aequipinnis*, *A. gouldii* and *B. frenchii*, respectively, from that environment (Coulson *et al.*, 2009, 2012; Cossington *et al.*, 2010).

Although small *O. dentex*, *i.e.* <150 mm L_T, were never observed, let alone caught, the plots of the lengths at age of the females and males imply that both sexes of this species grow rapidly and presumably in an approximately linear fashion during the first 4–5 years of life. By the end of that period, both sexes are approaching the values of 345 and 356 mm for the L_{T50} for females and males and are regularly being caught. These trends, and the failure to observe or catch younger fish, suggest that, as the individuals of *O. dentex* approach their size at maturity (c. 350 mm L_T), they tend to move to around reefs and thus become more visible to spear fishers. Presumably, the early juveniles of *O. dentex* reside deeper within the caves and crevices of reefs, where they would receive greater protection from the numerous piscivorous fish species that live around these reefs (Platell *et al.*, 2010). Other species in south-western Australia, such as the West Australian dhufish *Glaucosoma hebraicum* Richardson 1845 and the King George whiting *Sillaginodes punctata* (Cuvier 1829), also change habitat when they approach their lengths at maturity of c. 300 and 400 mm, respectively, but these are more extreme as they involve a movement to around reefs from over flat hard substrata with the first species and from over sand or in seagrass with the second species (Hyndes *et al.*, 1998; Hesp *et al.*, 2002).

Both sexes of *O. dentex* have greater maximum ages than those which, on the basis of their ages at 50% maturity, would be expected from the equation of Froese

TABLE V. Examples of species of Serranidae for which maximum ages have been recorded, together with the maximum lengths (total length, except * standard and † fork lengths) of those species in their respective studies

Species	Maximum length (mm)	Maximum age (years)	Validation	Reference
Othos dentex	605	37	m	Present study
Epinephelides armatus	510	19	m	Moore *et al.* (2007)
Centropristis striata	278	7	m	Hood *et al.* (1994)
Diplectrum formosum	236*	8	m	Bubley (2004)
Diplectrum pacificum	219*	4	n	Bortone (1977)
Paralabrax auroguttatus	479*	24	n	Pondella *et al.* (2001)
Paralabrax clathratus	580	33	n	Love *et al.* (1996)
Paralabrax maculatofasciatus	322*	11	e	Andrews *et al.* (2005)
	400*	14	e	Allen *et al.* (1995)
Paralabrax nebulifer	620	24	n	Love *et al.* (1996)
Serranus atricauda	432	16	e	Tuset *et al.* (2004)
Serranus cabrilla	210	5	m	Tserpes & Tsimenides (2001)
	223†	4	n	Torcu-Koc *et al.* (2004)
Serranus hepatus	140	5	s	Labropoulou *et al.* (1998)
	130	7	s	Dulčić *et al.* (2007)

m and e, age validation by marginal increment and edge analysis of otoliths; s, scales used for ageing; n, ages based on number of opaque zones in otoliths, but not validated.

& Binohlan (2000). This suggests that, as with the co-occurring protogynous labrid *B. frenchii*, which matures at only 5 years of age and yet can live for as long as 78 years (Cossington *et al.*, 2010), maturity is attained at an earlier age than would be expected given their longevity. The lengths of both sexes of *O. dentex* at maturity are consistent, however, with those that would be expected from their asymptotic lengths. This feature, in combination with the earlier than expected age at maturity, suggests that the growth of *O. dentex* prior to maturity is particularly rapid. While another co-occurring species, the long-lived and gonochoristic *S. aequipinnis* attains maturity at an age consistent with that expected given its maximum age, the length at which it attains maturity is far greater than would be predicted from its asymptotic length (Coulson *et al.*, 2012). This again reflects particularly rapid growth to the size at which maturity is attained. The highly cryptic nature of juvenile *O. dentex*, and that of *B. frenchii* (S. Cossington, unpubl. data), could provide an adaptation that would reduce the potential for predation early in life, and thereby augment the benefits of any selection pressure for rapid growth in that period.

The mortality estimates, derived for both sexes of *O. dentex* using the equations of Chapman & Robson (1960), clearly indicate that the larger and older individuals of this anthiine are subjected to relatively low levels of total mortality. The estimates of Z, obtained using the equation of Hoenig (1983) and which is often used to provide values taken as estimates of natural mortality, suggest that fishing mortality (*i.e.* the difference between total and natural mortality) on *O. dentex* is light, *i.e. c.* 30% of natural mortality. This is consistent with the fact that the amount of fishing for this

recreational species along the coast is low. Furthermore, the above value of 30% for fishing mortality as a percentage of natural mortality for *O. dentex* is appreciably lower than the corresponding value of *c*. 70%, derived for another long-lived and co-occurring species that is fished commercially in those waters, *i.e. A. gouldii* (Coulson *et al.*, 2009).

SPAWNING PERIOD AND SEXUAL DICHROMATISM

The trends exhibited by the mean monthly I_G and monthly percentage frequencies of occurrence of sequential gonad stages of both sexes demonstrate that the spawning period of *O. dentex* extends from September to March and peaks between November and January. Certain other serranids also have a protracted spawning period (Sadovy, 1996), including *E. armatus* which spawns for the same duration in waters off the lower west coast of Australia (Moore *et al.*, 2007). In contrast, the spawning duration of some other commercially and recreationally important co-occurring and reef-dwelling demersal fish species on the cool south coast of Western Australia is shorter, ranging from 2 or 3 months in silver seabream *Pagrus auratus* (Forster 1801) and *S. aequipinnis* to 5 months in *B. frenchii* and *A. gouldii* (Wakefield, 2006; Coulson *et al.*, 2009, 2012; Cossington *et al.*, 2010). A protracted spawning period and indeterminate fecundity over a long life span ensures that large numbers of eggs are produced during a spawning season and that some will therefore be released at times likely to be favourable for egg and larval survival (McEvoy & McEvoy, 1992).

This study has developed a novel method to track quantitatively the body colouration of the females and males during the change from juvenile to adult. The data in Fig. 9 demonstrate that, on the lower half of the body of *O. dentex*, the large spots are yellow in all juveniles and that this colour is retained throughout adult life by females, whereas the colour of the corresponding spots in males changes rapidly to green and then to blue as this sex attains and passes the size at maturity. Although the blue colour is retained by the spots throughout the adult life of males, it intensifies greatly during the spawning period and peaks at the mid-point of this period. The fact that the change to blue of the spots on males occurs at around the length at which this sex becomes mature and intensifies during spawning strongly suggests that this change is related to increases in androgen levels, as recorded for numerous sexually dimorphic actinopterygians (Kodric-Brown, 1998; Mank, 2007). In a review of sexual dichromatism in fishes, Kodric-Brown (1998) noted that, when piscivorous predators are absent, sexual selection has favoured the development of conspicuous, complex colours and patterns that contrast with the background. In such environments, the spots are large and numerous and overall body colour is diverse, as with adult *O. dentex*. The quantitative demonstration that the change in colour of the prominent spots on the males of *O. dentex* occurs abruptly at around the length corresponding to the L_{T50} implies that this species would provide a particularly good model for exploring the precise relationship between this type of change and the levels of circulating androgens.

Nuptial colour patterns are known to enhance courtship behaviour in fishes (Kodric-Brown, 1998) and have been identified in serranids other than *O. dentex* (Erisman & Allen, 2006). These observations, in conjunction with the development of blue spots by the males of certain territorial fishes associated with the acquisition and defence of a territory (Kodric-Brown, 1998), strongly suggest that the

intensification of the blue colouration of the spots of the adult males of *O. dentex* during the spawning period plays a role in courtship and agonistic behaviour. Underwater observations emphasize that the males of this species are typically solitary, apart from during the spawning season when a male and a female are sometimes seen together (B. French, unpubl. obs.).

While this implication that *O. dentex* is a pair spawner is consistent with its males having a very low I_G (Sadovy & Colin, 1995; Molloy *et al.*, 2007), this is unusual for a gonochorist of a serranid or related family (Erisman *et al.*, 2009). In this context, it is particularly noteworthy that the males of the co-occurring and likewise gonochoristic anthiine *E. armatus* also possess very small testes and that this led to the conclusion that this species is also likely to be a pair spawner (Moore *et al.*, 2007). Note that the values for the tick marks on the *y*-axis for the I_G for male *E. armatus* in Fig. 5 of Moore *et al.* (2007) should have been labelled at 0·04 intervals, between 0 and 0·16, with the mean maximum monthly I_G for males thus being <0·12.

The possession of small testes by *O. dentex* and *E. armatus*, which implies relatively low sperm competition (Molloy *et al.*, 2007), is unusual for gonochoristic members of Serranidae (Erisman *et al.*, 2009). Indeed, those characteristics are typically found in species that are protogynous hermaphrodites and spawn in pairs (Erisman *et al.*, 2009). According to the size advantage hypothesis (Ghiselin, 1969), selection for protogyny should be an advantage in those polygamous mating systems where large males monopolize mating with females (Warner, 1975, 1984, 1988; Erisman *et al.*, 2009; Kazancioğlu & Alonzo, 2010). In contrast, and apart from *O. dentex* and *E. armatus*, gonochorists in the Serranidae and closely related families typically spawn in groups and such spawning involves intense sperm competition (Warner, 1984; Erisman *et al.*, 2009). Thus, the trends exhibited by the above reproductive characteristics of *O. dentex* and *E. armatus* run counter to those considered characteristic of those families. It is tentatively proposed that, at least in the case of *O. dentex*, the spawning of this anthiine in pairs rather than in substantial groups, as with other gonochoristic members of the Serranidae and closely related Epinephilidae, reflects the fact that this species is not superabundant on the south coast of Western Australia and its individuals are widely dispersed. In this case, there would be little selection pressure for the development of a large testis as sperm competition is presumably limited.

In summary, this integrated study of the reproductive characteristics of *O. dentex* has demonstrated definitively that this species (1) is an atypical anthiine in that it is a gonochorist rather than a protogynous hermaphrodite, (2) develops marked sexual dichromatism at maturity and (3) matures at a relatively young age given its considerable longevity. This study also shows that *O. dentex* is unusual for a gonochoristic serranid and related families in that its males have a low I_G and which, together with underwater observations of the individuals of this species, strongly indicate that it is a pair spawner. The above findings and conclusions parallel, however, those for the gonochoristic anthiine *E. armatus*, apart from the fact that this latter species does not develop marked sexual dichromatism as an adult. The gonochorism exhibited by *O. dentex* and *E. armatus*, together with the lack of a central 'ovarian' lumen and peripheral sperm sinuses in their testes, contrasts with the situation typically found in other anthiines and serranids in general (Sadovy de Mitcheson & Liu, 2008; Erisman & Hastings, 2011). The demonstration that the colour of the prominent spots of the males of *O. dentex* changes quantitatively and abruptly at around L_{T50} for maturity

of this species and that the colour intensifies during the spawning period implies that this species would provide a particularly good model for exploring the ways in which the development of this form of sexual dichromatism is related to circulating androgen levels and is reflected in the behaviour of the males.

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