Abstract—The western blue groper (*Achoerodus gouldii*) is shown to be a temperate protogynous hermaphrodite, which spawns between early winter and mid-spring. Because *A. gouldii* changes body color at about the time of sex change, its color can be used as a proxy for sex for estimating the size and age at sex change and for estimating growth when it is not possible to use gonads for determining the sex of this fish. The following characteristics make *A. gouldii* highly susceptible to overfishing: 1) exceptional longevity, with a maximum age (70 years) that is by far the greatest yet estimated for a labrid; 2) slow growth for the first 15 years and little subsequent growth by females; and 3) late maturation at a large total length (TL_{50}=653 mm) and old age (~17 years) and 4) late sex change at an even greater total length (TL_{50}=821 mm) and age (~35 years). The TL_{50} at maturity and particularly at sex change exceeded the minimum legal total length (500 mm) of *A. gouldii* and the lengths of many recreationally and commercially caught fish. Many of these characteristics are found in certain deep-water fishes that are likewise considered susceptible to overfishing. Indeed, although fishing effort for *A. gouldii* in Western Australia is not particularly high, per-recruit analyses indicate that this species is already close to or fully exploited.

The western blue groper (*Achoerodus gouldii*), a protogynous hermaphroditic labrid with exceptional longevity, late maturity, slow growth, and both late maturation and sex change

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Species of the family Labridae, which represents one of the largest and most speciose of all perciform families (comprising 82 genera and at least 600 species) are found in tropical and temperate coastal and continental shelf waters throughout the world (Westneat and Alfaro, 2005; Allen et al., 2006). On the basis of demographic analyses of large labrid species, Choat et al. (2006) concluded that they are characterised by relatively short life spans and indeterminate growth rates, namely, growth does not tend to an asymptote. However, a few species have substantial life spans; the oldest ages yet recorded for a labrid are 30–35 years (Gillanders, 1995a; Choat and Robertson, 2002; Choat et al., 2006).

Most of the biological studies on labrids have been undertaken on subtropical and tropical species (Denny and Schiel, 2002). These studies have shown that many members of this family are protogynous hermaphrodites, namely they change from female to male (e.g., Reinboth, 1970; Candi et al., 2004; McBride and Johnson, 2007). Sex change in these labrids is often accompanied by a change in body color and they are thus sexually dichromatic (Warner and Robertson, 1978; Shapiro, 1981; Gillanders, 1995a). Among labrids, a few species change from one sex to another and then back again, and thus undergo

what is termed reversed sex change (Ohta et al., 2003; Kuwamura et al., 2007), and a number are gonochoristic, i.e., do not undergo sex change (Dipper and Pullin, 1979; Bentivegna and Benedetto, 1989; Sadovy de Mitcheson and Liu, 2008). However, a recent study of the green humphead parrotfish (*Bolbometopon muricatum*) has emphasised that a definitive conclusion as to whether certain species in this family are protogynous hermaphrodites or gonochorists can be difficult to ascertain, even when there is detailed information on such features as the size compositions of the two sexes and the histological characteristics of their gonads (Hamilton et al., 2008).

The western blue groper (*Achoerodus gouldii*) is found throughout southern Australia, southwards from the Houtman Abrolhos Islands at 28°30′S, 113°40′E on the west coast and eastwards along the south coast to Portland in Victoria at 38°21′S; 141°36′E (Hutchins and Swainston, 1986; Gommon et al., 1994) but is most abundant on the south coasts of Western Australia and South Australia. This species is reported to attain a maximum length of 175 cm (Gommon et al., 1994), which, among labrids, is apparently exceeded only by the humphead wrasse (*Cheilinus undulates*) (Sadovy et al., 2003). Although *A. gouldii* is the second most

commercially important species of scale fish on the south coast of Western Australia and is highly regarded by recreational anglers, detailed studies of its biology have been restricted to its foraging behavior, diet, and habitat, and how these change with body size (Shepherd, 2005; Shepherd and Brook, 2007). In contrast, several aspects of the biology of the congeneric eastern blue groper (*Achoerodus viridis*), which is distributed along the eastern and southeastern coasts of Australia and does not grow to as large a size as that of *A. gouldii* (Hutchins and Swainston, 1986), have been studied (e.g., Gillanders, 1995a, 1995b, 1997; Gillanders and Kingsford, 1998). The apparently detrimental effects of fishing on *A. viridis* led to this species being protected from both recreational and commercial fishing in 1969, although these restrictions were later eased to some extent in 1974 (Gillanders, 1999).

The present study demonstrates that *A. gouldii* is a protogynous hermaphrodite and provides data on the length and age compositions, growth, reproductive biology, recruitment variability, and stock status (mortality, and spawning potential ratio) of this species in southwestern Australian waters. The data were used to test the following hypotheses. 1) The far greater size of *A. gouldii* than the morphologically and ecologically similar congeneric eastern blue groper (*Achoerodus viridis*) is reflected in a greater maximum age and greater sizes and ages at which females become mature and later change sex. 2) It would then follow that *A. gouldii* has by the greatest longevity of any labrid species. Because protogynous labrids that exhibit sexual dichromatism tend to change color at about the same size and age as at which sex change occurs, the body colors of *A. gouldii* (typically green for females and blue for males) can be used as proxies for sex for determining the total length at which 50% of fish (TL_{50}) change color and the patterns of growth of females and males of this labrid. An ability to use color in this manner would be useful when, for example, fish cannot be dissected or the viscera have been removed. 3) Because environmental factors on the southwest coast of Australia, such as those brought about by marked variations in the strength of the Leeuwin Current (Pearce and Phillips, 1988), exhibit considerable interannual variations in winter, i.e., when *A. gouldii* spawns (see *Results* section), the recruitment success of this species on this coast differs among years. Lastly, inferences drawn from the biological data and stock assessment parameters are discussed for their applicability to management plans aimed at conserving the stocks of *A. gouldii*.

Materials and methods

Sampling regime and laboratory processing

Achoerodus gouldii was collected monthly or bimonthly between April 2004 and October 2007 from numerous sites in coastal waters between Albany (at 35°01′S, 117°58′E) and Esperance (at 33°45′S, 21°55′E) off the south coast of Western Australia. These fish were either caught by spear fishing in shallow (<20 m) inshore coastal waters or were obtained from commercial gill net fishing crews (mesh range=165–178 mm) operating in deeper (~20–100 m) offshore waters. A few *A. gouldii* (~3%) were also collected directly from commercial gillnet fishing vessels fishing in deeper, offshore waters at a latitude of ~32°S on the lower west coast of Australia. Although many of the individuals obtained from commercial gillnet fishing vessels were supplied as eviscerated and filleted frames, some were intact and therefore still contained their gonads.

Shallow, inshore water temperatures at Albany and Esperance, recorded by the Department of Fisheries, Western Australia, at intervals in the years 1994–2006, were pooled by month and used to calculate the average for each calendar month. Mean monthly offshore sea surface temperatures for Albany and Esperance in 2004–06 were derived by using a combination of data from National Oceanic and Atmospheric Administration (NOAA) advanced very high resolution radiometer (AVHRR) satellite imagery and from sea surface temperatures recorded by shipping and drifting buoys (Reynolds and Smith, 1994). The mean monthly water temperatures in inshore and offshore waters in the above two main sampling locations were plotted to elucidate the relationship between the initiation and duration of spawning and water temperature, which are typically related in teleosts (e.g., Lam, 1983).

The color (green or blue) and total length (TL, to the nearest 1 mm) of all *A. gouldii*, and the wet weight (W, to the nearest 0.1 g) of each of those individuals that had not been filleted, eviscerated, (or both), were recorded. The sex of each *A. gouldii* that had not been eviscerated and had a TL >~100 mm (the length above which the sex could be determined macroscopically) was also recorded. Because all of the large number of sexed fish <655 mm were females (see *Results*), the small number of fish <100 mm were recorded as this sex. Although the possibility cannot be excluded that some of the latter very small *A. gouldii* (<100 mm) may have been bisexual (i.e., possessed gonads containing both ovarian and testicular material), the fact that all individuals between the substantial length range of 100–655 mm were females means that this attribute would not have influenced the conclusions regarding whether this species is hermaphroditic and, if so, of which type (see *Discussion*). The gonads of each fish were removed and weighed to the nearest 0.01 g.

The relationship between TL and W was used to estimate the weights of *A. gouldii* collected from fish processors and recreational fishing crews and which had been filleted, eviscerated, or both, before they could be weighed. To facilitate comparisons between the lengths of *A. gouldii* and those of its congener *A. viridis*, the latter of which were recorded as standard lengths to the nearest 1 mm by Gillanders (1995a), standard lengths for 455 *A. viridis* were converted to total lengths by using the equation

$$TL = 1.19(SL) + 7.93,$$

where *TL* = total length;
      SL = standard length; and

for which the value of the coefficient of determination was 0.99 (*P*<0.001).

Note that, because the tail of *A. gouldii* is not forked, the TL and fork lengths (FL) of this species are the same and thus the TL for this species can be compared directly with the fork lengths recorded for other labrid species (e.g., Choat et al., 2006).

Aging methods, length and age compositions, and growth patterns

Preliminary examination of the otoliths of a wide size range of *A. gouldii* before and after sectioning demonstrated that even the otoliths of small fish required sectioning to reveal all of their opaque zones. One sagittal otolith from each individual was embedded in clear epoxy resin and a section of ~0.3 mm thickness was cut transversely through the primordium with an Isomet Buehler low-speed diamond saw (Buehler Ltd., Lake Bluff, IL). The otolith sections were polished with wet and dry carborundum paper (grade 1200) and mounted on microscope slides with DePeX mounting adhesive (VWR International Ltd., Poole, England) and a cover slip. Electronic images of each section of otolith and of its peripheral region (at a higher magnification) were taken with transmitted light and an Olympus DP70 camera (Olympus Optical Co. Ltd., Tokyo, Japan) mounted on an Olympus BX51 compound microscope (Olympus Optical Co. Ltd., Tokyo, Japan). These images were used for counting opaque zones and measuring the distances required for marginal increment analysis, respectively. All images were examined by using Leica Image Manager 1000 (Leica Microsystems, Heerbrugg, Switzerland), which enabled the well-defined opaque zones (Fig. 1) to be marked and automatically counted and the distances required for marginal increment analysis to be measured precisely.

Validation that a single opaque zone is formed annually in the otoliths of *A. gouldii* was carried out by analyzing the trends exhibited throughout the year by the marginal increment on the otoliths, i.e., the distance between the outer edge of the single or outermost opaque zone and the otolith periphery. The marginal increment was expressed as the proportion of the distance between the primordium and the outer edge of the opaque zone, when one such zone was present, or as the proportion of the distance between the outer edges of the two outermost opaque zones when two or more such
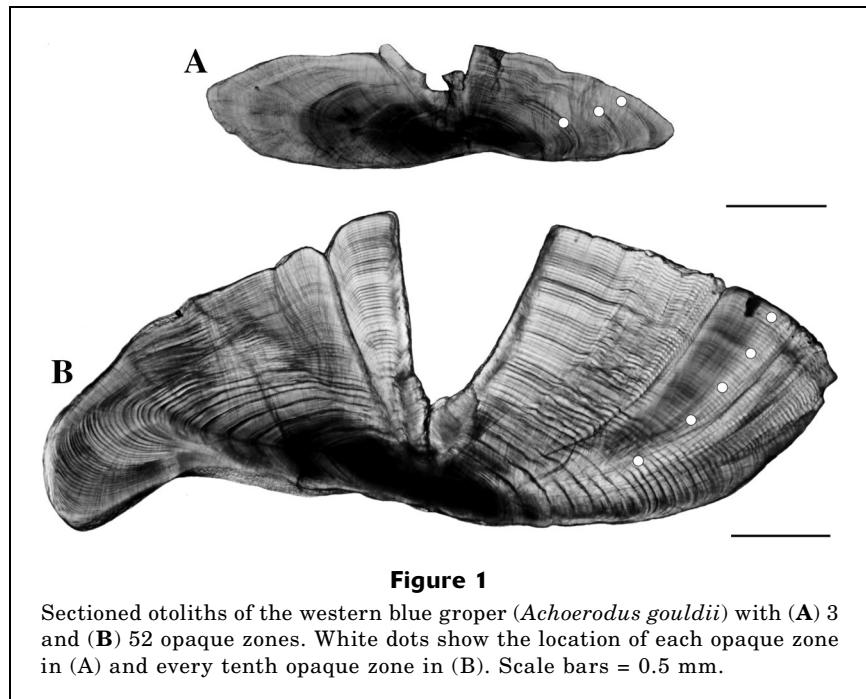
Figure 1

Sectioned otoliths of the western blue groper (*Achoerodus gouldii*) with (**A**) 3 and (**B**) 52 opaque zones. White dots show the location of each opaque zone in (A) and every tenth opaque zone in (B). Scale bars = 0.5 mm.

zones were present. All distances, which were recorded to the nearest 0.01 mm, were measured on the anterior surface of the otoliths and along the same axis as and perpendicular to the opaque zones.

The opaque zones on the anterior surface in an image of each sectioned otolith were counted on three different occasions. The three counts were the same in 91.0% of otoliths with ≤20 opaque zones and 70.4% of those with >20 opaque zones. In the case of each otolith for which the three counts were not the same, if two of those counts were the same, these counts were the ones recorded for aging. The numbers of opaque zones in 150 otoliths from a wide size range of fish were counted by a second and experienced otolith reader (S. A. Hesp) and compared with those recorded by the senior author. The counts of 70 of the 100 otoliths with ≤20 opaque zones were the same and, where there were discrepancies, they differed by only 1 in 28 of the otoliths and 2 in the other two otoliths. For the 50 otoliths containing >20 opaque zones, the counts were the same or differed by 1 in 34 of those otoliths and differed by no more than 2 in a further seven otoliths. The maximum difference in the counts for otoliths with >20 opaque zones was 4. Following discussions between the two readers, it became apparent that the main reason for discrepancies in counts was due to the first reader, who through his extensive experience of examining the otoliths of *A. gouldii*, was able more consistently to detect the first zone. The level of agreement between the counts of the two readers was therefore high when his experience in detecting the first zone was taken into account.

Each fish was assigned an age based on its date of capture, the number of opaque zones in its otoliths, the time of year when newly formed opaque zones become

delineated from the otolith periphery, and on an appropriate birth date for *A. gouldii* (see *Results*). The von Bertalanffy growth equation, used for describing the growth of *A. gouldii*, **is**

$$L_t = L_\infty \left(1 - \exp^{(-k(t-t_0))}\right),$$

where L_t = the length (mm TL) at age t (years);
$\quad\quad L_\infty$ = the mean asymptotic length (mm) predicted by the equation;
$\quad\quad k$ = the growth coefficient (per year); and
$\quad\quad t_0$ = the hypothetical age (years) at which fish would have zero length.

Von Bertalanffy growth curves were fitted to the lengths at age of *A. gouldii* in the cases of 1) all fish irrespective of their sex; 2) females and males that had been sexed on the basis of an examination of their gonads; and 3) those fish that were a mixture of green and blue among the individuals used for constructing the growth curves for each sex in 2 (the above growth curves were fitted by using nonlinear regression in the Statistical Package for the Social Sciences, SPSS (vers. 11.0, SPSS Inc., Chicago, IL); and 4) von Bertalanffy growth curves for each sex were next fitted to the combination of the lengths at age of sexed and unsexed individuals, taking into account the probability that, from its total length and color, an unsexed fish would be a male or a female. For each unsexed fish, the expected length, $\hat{L}_j^s$, was first calculated as

$$\hat{L}_j^s = \begin{cases} L_\infty^f \left(1 - \exp\left[-k^f \left(t_j - t_0^f\right)\right]\right) & \text{if } s = f \text{ or } t_j \leq t_{\text{diverge}} \\ L_\infty^m \left(1 - \exp\left[-k^m \left(t_j - t_0^m\right)\right]\right) & \text{if } s = m \text{ and } t_j > t_{\text{diverge}} \end{cases},$$

where $\quad s$ = sex ($s = f$ for a female and m for a male);
$\quad\quad t_j$ = the age of fish j;
$\quad\quad t_{\text{diverge}}$ = the age at which it was assumed that female and male growth curves began to diverge;
$\quad L_\infty^f$ and L_∞^m = the mean asymptotic lengths for females and males, respectively;
$\quad k^f$ and k^m = the growth coefficients for females and males, respectively; and
$\quad t_0^f$ and t_0^m = the hypothetical ages at which, assuming growth in accordance with the above von Bertalanffy growth equations, females and males, respectively, would have zero length.

Note that, if $L_{diverge}$ is the expected length of the females at age $t_{diverge}$, then

$$t_0^m = t_0^f - \left(1/k^f\right)\log_e\left[1 - \left(L_{\text{diverge}}/L_\infty^f\right)\right] + \left(1/k^m\right)\log_e\left[1 - \left(L_{\text{diverge}}/L_\infty^m\right)\right],$$

where $\log_e$ = the natural logarithm.

The observed lengths at age of fish were assumed to be normally distributed about the predicted lengths at age for each sex, and to have a common standard deviation.

The probability that fish j was of sex s was denoted by p_j^s, where $p_j^f = 1 - p_j^m$ and where $p_j^m = 1$ if the fish possessed testes, $p_j^m = 0$ if the fish possessed ovaries and p_j^m = the value calculated with the logistic equation presented in the next section if the fish had been eviscerated and sex could not therefore be determined. The value of the normal probability density function, for fish j of sex s, ϕ_j^s, was calculated as

$$\phi_j^s = 1/\left(\sqrt{2\pi\, sd^2}\right)\exp\left[-\left(\left(L_j - \hat{L}_j^s\right)^2\right)/\left(2\, sd^2\right)\right],$$

where $\quad L_j$ = the observed length at age;
$\quad\quad \hat{L}_j^s$ = the predicted length at age;
$\quad\quad sd$ = the standard deviation; and
$\quad\quad \pi$ = the constant pi.

The log-likelihood, λ, determined as $\sum_j \log_e\left(\sum_s p_j^s \phi_j^s\right)$, was maximized by using Solver in Microsoft Excel to estimate the parameters L_∞^f, k^f, t_0^f, L_∞^m, k^m, $t_{diverge}$, and sd. Approximate 95% bootstrap confidence limits of the parameters were calculated as the 2.5 and 97.5 percentiles of the parameter estimates obtained by fitting the model to 1000 resampled data sets.

Reproductive biology

The gonadosomatic index (GSI) of each female with a length $\geq$ the TL_{50} at maturity (see *Results*) was calculated as

$$GSI = (W_1/W) \times 100,$$

where W_1 = wet gonad weight; and
$\quad\quad W$ = wet body weight.

The criteria of Moore et al. (2007), adapted from Laevastu (1965), was used to allocate each gonad to one of the following maturity stages, I = virgin; II = immature or resting; III = developing; IV = maturing; V = prespawning; VI = spawning; VII = spent; and VIII = recovering or spent. Note that the TL_{50} at maturity was used as the cut off for determining the GSI of individuals because, outside the spawning period, it was not possible macroscopically to distinguish the gonads of virgins (stage I) from those of fish that had matured but were in a resting state (stage II).

Gonads from a large subsample of females and males in each month were placed in Bouin's fixative for 24 to 48 hr—the duration depending on the size of the gonad. They were then dehydrated in a series of increasing concentrations of ethanol and their mid-regions were embedded in paraffin wax and cut into 6-μm transverse sections, which were stained with Mallory's trichrome. The histological characteristics of the ovaries in that large subsample (see Coulson et al., 2005) were used to

validate the macroscopic staging. Note that comparisons of transverse sections through the anterior, middle, and posterior regions of the gonads of 10 *A. gouldii* over a wide size range demonstrated that the characteristics of those gonads remained similar throughout their length.

The length at which 50% of female *A. gouldii* attained maturity (TL_{50}) was determined by fitting a logistic curve to the probability that, during the spawning period, a female fish at a specific length would possess gonads at one of stages III to VIII. As such fish were potentially destined to become mature or had reached maturity during that period (see *Results*), they are, for convenience, referred to as mature in the present study. The logistic equation used for this analysis was

$$P = 1 / \left\{ 1 + \exp\left[-\log_e(19)(TL - TL_{50}) / (TL_{95} - TL_{50}) \right] \right\},$$

where P = proportion mature;
TL = total length in mm; and
TL_{50} and TL_{95} = the total lengths in mm at which 50% and 95% of fish were mature, respectively.

The logistic equation was fitted by using Markovian chain Monte Carlo simulation in WinBUGS (vers. 1.4.3, MRC Biostatistics Unit, Cambridge, U.K.) from 500,000 iterations, discarding the first 1000 iterations as the initial burn in set and using a thinning interval of 100 iterations. After assessment in WinBUGS that convergence was likely to have been achieved, the point estimates of the parameters of the logistic equation and their 95% confidence intervals, and of the probabilities of fish being mature at a range of specified lengths, were determined as the medians and the 2.5 and 97.5 percentiles of the estimates produced by WinBUGS.

Because the six fish with gonads containing both testicular and ovarian tissue all had lengths that lay within the range where the prevalence of females was decreasing and that of males was increasing, they were considered likely to be changing from female to male. Because the testicular tissue in those fish was more mature than the ovarian material, the data for these fish were combined with those for male *A. gouldii* for determining the length and age at which *A. gouldii* change sex. WinBUGS was then used as above to estimate the TL_{50} and TL_{95} for change in both sex and color, i.e., from green to blue (from female to male).

Logistic regression analysis was employed to relate the probability, p_j^m, that fish j was a male to its length L_j and color C_j (green=0, blue=1). p_j^m was determined as

$$\left[1 + \exp\left(-\alpha - \beta_1 L_j - \beta_2 C_j \right) \right]^{-1},$$

where α, β_1, and β_2 are constants.

The probability that fish j possessed female gonads, p_j^f, was determined as $p_j^f = 1 - p_j^m$. The Akaike information criterion (AIC) (Burnham and Anderson, 2002) was used to determine which of the models, based solely on either length ($\beta_2 = 0$) or color ($\beta_1 = 0$), provided the better predictions. The AIC is determined by the following equation:

$$AIC = -2\lambda + 2K,$$

where λ = the log-likelihood; and
K = number of parameters.

The model with the lowest AIC value was selected as the better of the two models. The likelihood-ratio test (Cerrato, 1990) was then used to determine whether the model that contained both length and color significantly improved the prediction that a fish was a male.

Recruitment variability, mortality, and spawning potential ratio

The number of fish in each year class in each of three successive annual periods was determined. Because 1 August coincides with the birth date designated for *A. gouldii*, these estimates of numbers encompassed each of the three successive 12-month periods between 1 August and the following 31 July in the years 2004 to 2007.

Total mortality, Z, for *A. gouldii* was estimated from the age compositions of samples of fish collected during the above three successive 12-month periods (years) by using catch curve analysis and then relative abundance analysis (see below). We used data obtained from the commercial gillnet fisheries and assumed knife-edge recruitment into the fishery at 15 years, i.e., we restricted data to those for the descending limbs of the catch curves (Ricker, 1975).

Initially, an estimate of Z was calculated by using catch curve analysis, where recruitment was assumed to be constant. For a fish stock that experiences a constant level of Z from the age of full recruitment, $a = t_c$ years, the estimated proportion, $\hat{P}_{a,t}$, of fish at age a in year t is

$$\hat{P}_{a,t} = \left\{ R_{t-a} \exp\left[-(a - t_c)Z \right] \right\} / \left\{ \sum_{j=t_c}^{A} R_{t-j} \exp\left[-(j - t_c)Z \right] \right\},$$

where A = the maximum observed age;
j = an index of age, where $t_c \leq j \leq A$;
R_{t-a} = the number of fish of year class $t - a$ that recruited at age t_c years to the fully vulnerable portion of the fish stock in year $t-a+t_c$, and which, in year t, are of age a years; and
R_{t-j} = the number of fish of year class $t - j$ that recruited at age t_c years to the fully vulnerable portion of the fish stock in year $t-j+t_c$, and which, in year t, are of age j years.

It is assumed that the age composition of fish with ages $t_c \leq a \leq A$ observed in year t represents a random sample from a multinomial distribution and uniform selectivity from the age of full recruitment. Thus, by ignoring constants, the log-likelihood, λ, of the age compositions observed in the various years may be calculated as

$$\lambda = \sum_t \sum_{a=t_c}^{A} n_{a,t} \log\left[\hat{P}_{a,t} \right],$$

where $n_{a,t}$ = the observed number of fish of age a in year t.

An estimate of Z was obtained by maximizing the log-likelihood by using Solver in Excel (vers. 2003, Microsoft Corporation, Salem, MA).

Next, the constraint that recruitment is constant in the analysis just described was relaxed and an estimate of Z was determined with relative abundance analysis (Deriso et al., 1985). This latter analysis, which is an extension of catch curve analysis, involved initially setting the relative level of recruitment, R_y, for each year class, y, to 1. The relative levels of recruitment of the different year classes were then successively introduced as additional parameters to be estimated by the model, by using a stepwise forward selection algorithm (e.g., Sokal and Rohlf, 1995). The process was terminated when the introduction of R_y as a parameter to be estimated for any further year class failed to produce a statistically significant improvement in the fit of the model to the data, as determined with the likelihood-ratio test (Cerrato, 1990). At each stage, the relative levels of recruitment for year classes not included as parameters to be estimated in the model continued to be constrained to the average level, i.e., 1. The 95% confidence intervals for Z for A. gouldii, when either constant or variable recruitment was assumed, were obtained from the profile likelihood for Z (Hilborn and Mangel, 1997). All of the above calculations for Z were undertaken by maximizing the above log-likelihood with the Solver tool in Excel.

The point estimate and 95% confidence intervals for the natural mortality, M, of A. gouldii were determined by refitting, in SPSS, Hoenig's (1983) regression equation for fish to the values for mortalities and maximum ages for 82 unexploited or lightly exploited fish stocks (see Hall et al., 2004) and including the maximum recorded age for A. gouldii.

The approach of Hall et al. (2004) was used to determine the likelihood for M, calculated by using the likelihood for Z, as derived by using the relative abundance analysis and assuming variable recruitment. For this estimation it was assumed that, for each value of Z, there is a uniform probability that $M < Z$. The resulting likelihood for M was then combined with the estimate for M derived by refitting Hoenig's (1983) regression equation for fish.

A Monte Carlo resampling approach was used to derive estimates of F for the fully recruited age classes of each species. Estimates of Z (from the relative abundance analysis) and M (from the method of Hall et al., 2004) were randomly resampled, with replacement, from their respective probability distributions, and any pair of estimates for which the value for M was greater than Z was rejected. 10,000 sets of estimates of Z and M were produced, from which 10,000 estimates of F were determined with the equation $F = Z - M$. The point estimate of F and associated 95% confidence limits were taken as the median value and the 2.5 and 97.5 percentiles of these estimates.

The spawning stock biomass per age-0 recruit (SSB/R) of A. gouldii was calculated for each sex with the equation

$$SSB/R = \sum_{a=t_c}^{A} W_a P_{sex,a} P_{mat,a} \exp(-Za),$$

where Z = total mortality;
W_a = the weight of a fish at age a;
$P_{sex,a}$ = the proportions of each sex at age a; and
$P_{mat,a}$ = the proportions of mature females at each age a.

W_a was calculated by using the von Bertalanffy growth curves for each sex and the relationship between total body weight (g) and length (mm). For males, $P_{sex,a}$ was determined by using the growth curve and the logistic relationship describing the probability that a fish of a given length is a male, whereas, for females, $P_{sex,a}$ was calculated as 1 minus this probability. $P_{mat,a}$ was determined by using the logistic function describing the probability that a fish of a given length is mature, together with the lengths at age predicted by using the von Bertalanffy growth function. All males were assumed to be mature. Estimates of SSB/R were determined for each of the 10,000 values generated for F by the resampling procedure. The point estimates and associated 95% confidence limits for the current level of SSB/R were taken as the median and 2.5 and 97.5 percentiles of the resulting SSB/R values. The spawning potential ratio, SPR, was calculated as the ratio of SSB/R at a specified level of fishing mortality to that for an unfished population (Goodyear, 1993). For the per-recruit analysis we assumed that knife-edge recruitment to the fishery occurred at 15 years, total mortality for fully recruited fish was constant and the maximum age was 100 years.

Results

Aging methods, length and age compositions, and growth pattern

The mean monthly marginal increments on sectioned otoliths of A. gouldii with 2–10 zones remained relatively high (≥ 0.39) between July and October, before declining sequentially to 0.36 in November and to a minimum of 0.26 in January and February, and then

rising progressively in the ensuing months (Fig. 2). Although the numbers of otoliths with one opaque zone in each month were far less, their mean values could still be seen to follow a similar annual trend. Although the mean monthly marginal increments on otoliths with 11–20, 21–30, and >30 zones followed trends that were very similar to those described for otoliths with 2–10 zones, the minima of the last two groups were reached later. Consequently, as the number of zones in otoliths increases, the new opaque zone in otoliths becomes visually detectable later, i.e., in late summer to early autumn, rather than in late spring to mid-summer. The similar single decline and subsequent progressive rise in mean monthly marginal increments, irrespective of the number of opaque zones, demonstrate that a single opaque zone is formed annually in the otoliths of *A. gouldii*. The numbers of opaque zones in otoliths could therefore be used for aging this species.

From the trends exhibited by the mean monthly GSIs and prevalence in each month of females with stages V and VI ovaries, the approximate mid-point of the spawning period was estimated to be August, i.e., the end of the Austral winter. The small fish caught in November were ~40 mm in length, and those captured in February and March were ~60 and 90 mm, respectively. The otoliths of the latter (Feb. and Mar.) two collections of fish contained no opaque zones, which is consistent with these fish, on average, having been spawned in late winter and therefore not having had the opportunity to lay down the opaque zone that is deposited annually during that season in older fish. The first of these zones becomes delineated in the spring of the second year of life, i.e., when fish are ~140 mm in length and ~18 months old.

The individuals in samples of *A. gouldii* ranged in total length from 40 to 1162 mm and in age from a few months to 70 years (Fig. 3). The largest and oldest *A. gouldii*, from which the gonads had not been removed and could therefore be sexed, were 880 mm and 49 years, for females, and 1134 mm and 57 years, for males.

Although the 822 *A. gouldii* collected by spear fishing ranged from 40 to 1050 mm TL, the majority of those individuals measured between 100 and 600 mm, a range of TLs that corresponds to ages 1 to 11 years (Fig 4). The 1107 *A. gouldii* obtained from the commercial gillnet fishery ranged from 428 to 1162 mm (TL) and from 6 to 70 years, but most were between 500 and 800 mm (TL) and 10 and 34 years (Fig. 3).

A von Bertalanffy growth curve provided a good fit to the lengths at age of *A. gouldii* (r^2=0.84; Table 1, Fig. 4A). On the basis of the von Bertalanffy growth equation, *A. gouldii* attain lengths of 335, 509, 678, 741, 764, and 773 mm by ages 5, 10, 20, 30, 40, and 50 years, respectively. The marked similarity in the estimated lengths at 30, 40, and 50 years of age reflects the markedly asymptotic pattern of growth of *A. gouldii,* with relatively little overall growth occurring after 15 years with females and 30 years with males.

The von Bertalanffy growth curves fitted separately to the lengths at age of sexed fish demonstrated that,
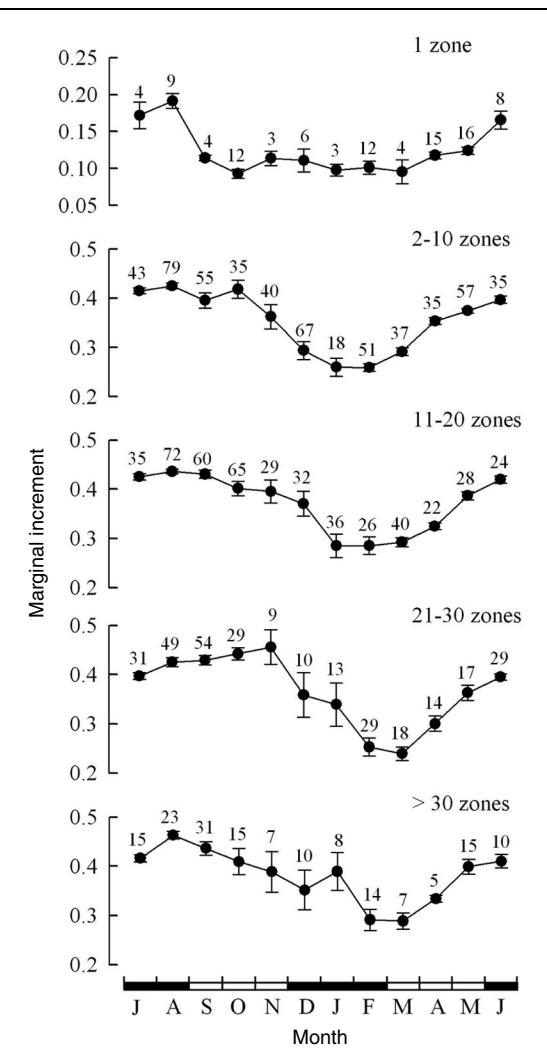
Figure 2

Mean monthly marginal increments ±1 standard error for sectioned sagittal otoliths of the western blue groper (*Achoerodus gouldii*) with different numbers of opaque zones. The marginal increment is expressed as a proportion of the distance between the primordium and the outer edge of the opaque zone, when one such zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones when two or more such zones were present. Sample sizes are shown above each mean. Closed rectangles on the *x*-axis refer to winter and summer months and the open rectangles to spring and autumn months.

after the age at which some females had changed to males, the growth curve for males increasingly diverged upwards from that for females (Fig. 4B). Thus, for example, at 20, 35, and 50 years, the estimated lengths at age for males were 805, 923, and 965 mm, respectively; whereas those for females were 679, 737, and 746 mm, respectively. The above differences in growth
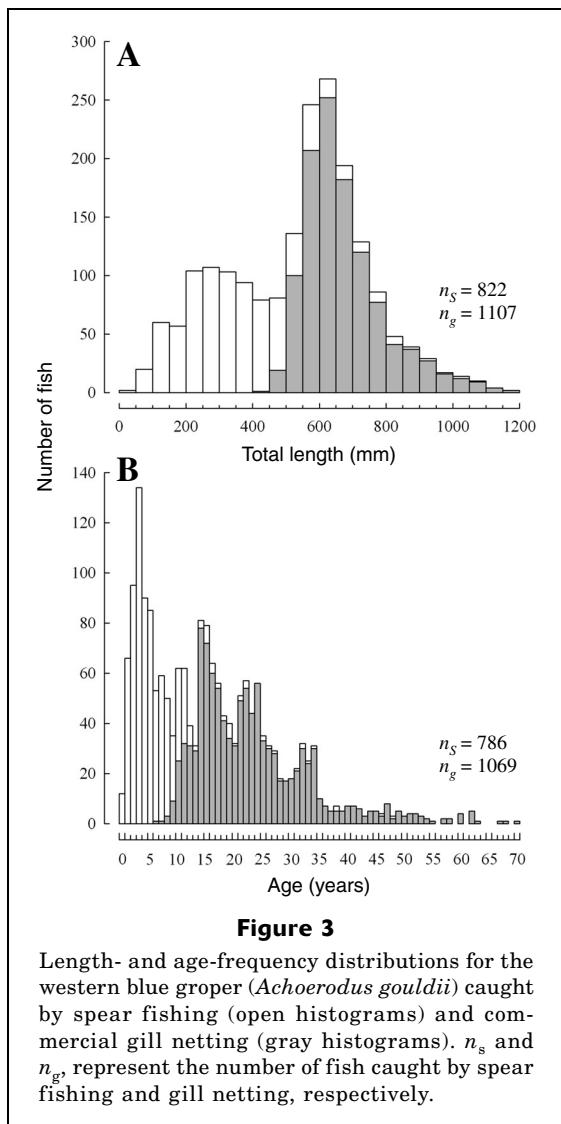
Figure 3

Length- and age-frequency distributions for the western blue groper (*Achoerodus gouldii*) caught by spear fishing (open histograms) and commercial gill netting (gray histograms). n_s and n_g, represent the number of fish caught by spear fishing and gill netting, respectively.

are reflected in a lower estimate for k for males (0.08/year) than for females (0.12/year), and in a reverse situation for L_∞, for which the respective values were 975 for males and 748 mm for females (Table 1).

When von Bertalanffy growth curves were fitted separately to the lengths at age of those individuals that were either green or blue, but that constituted the same subset of fish as those just used to describe the growth of males and females (Fig. 4B), the values for L_∞ and k for blue and for green fish were either identical or very similar to those for females and males, respectively (Fig. 4C; Table 1). Von Bertalanffy growth curves were next fitted to the lengths at age of fish, determined as females and males by using their gonadal characteristics (i.e., those used for Fig. 4B), and to the lengths at age of fish that could not be sexed by using gonads but could be assigned a sex on the basis of the combination of
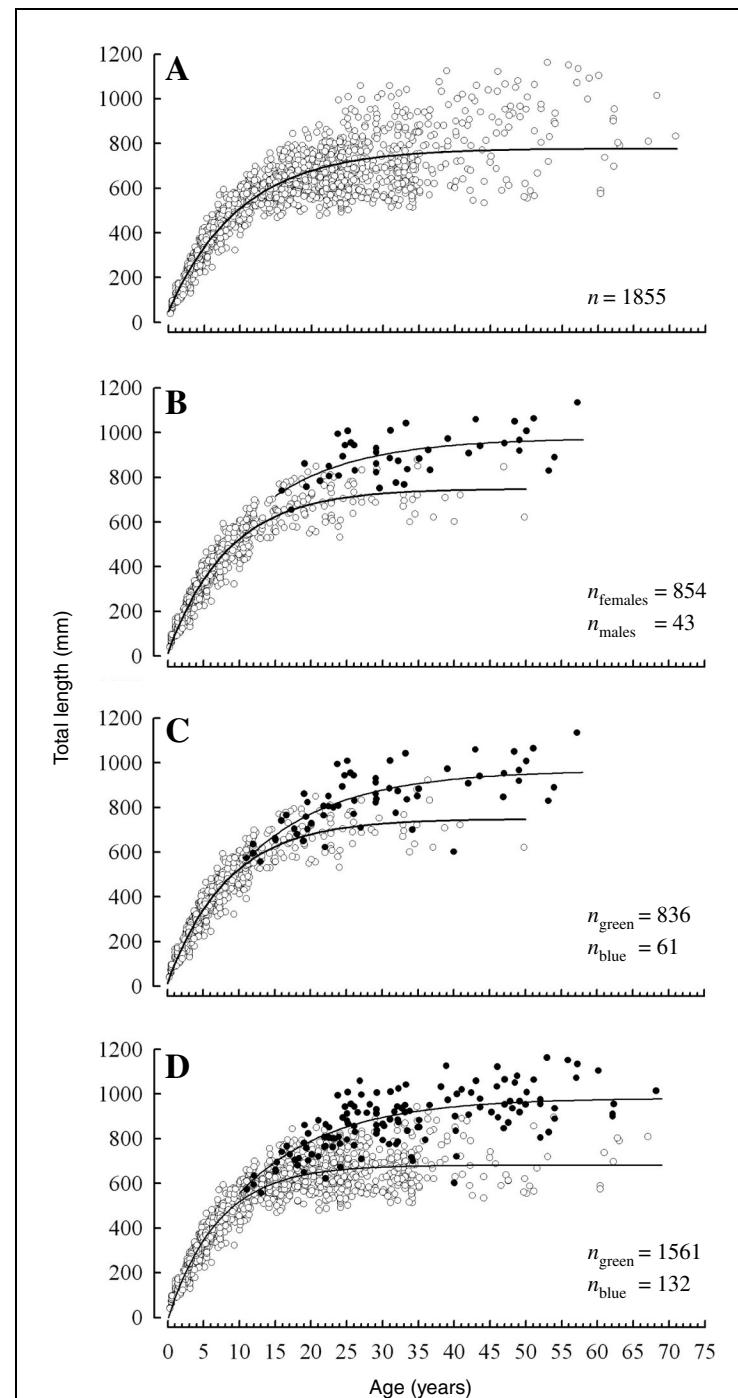
Figure 4

Von Bertalanffy growth curves fitted to the lengths at age of (**A**) all sexed and unsexed individuals, (**B**) females (open circles) and males (black circles) sexed on the basis of their gonadal characteristics, (**C**) the same individuals as in (B) but separated according to whether they were green (open circles) or blue (black circles), and (**D**) for females (open circles) and males (black circles), for which the sex of each individual had been designated by using either its gonadal characteristics or the probability of it being female or male on the basis of a combination of its body color and length. n = sample size.

Table 1

Estimates of the von Bertalanffy growth curve parameters L_∞, k, and t_0 (and their lower and upper 95% confidence limits [CLs]) for western blue groper (*Achoerodus gouldii*) caught off southwestern Australia (A) for all fish, (B) for females and males whose sex was determined from gonadal characteristics, (C) for the same fish as in B but according to whether they were green or blue, and (D) for fish whose sex was determined by using either gonad type or the likelihood of the fish being female or male on the basis of a combination of its length and color. L_∞ is the asymptotic length (mm), k is the growth coefficient (per year), t_0 is the hypothetical age (years) at which fish would have zero length, r^2 is the coefficient of determination, and n is the number of fish sampled.

Category			L_∞	k	t_0	r^2	n
A	All fish	Estimate	777	0.10	−0.65	0.84	1855
		Lower, upper CL	766, 789	0.09, 0.11	−0.90, −0.39		
B	Females	Estimate	748	0.12	−0.15	0.92	854
		Lower, upper CL	732, 764	0.11, 0.12	−0.30, 0.00		
	Males	Estimate	975	0.08	−0.91	0.35	43
		Lower, upper CL	879, 1072	−0.02, 0.19	−22.84, 21.03		
C	Green	Estimate	748	0.12	−0.17	0.92	836
		Lower, upper CL	731, 765	0.11, 0.12	−0.32, −0.02		
	Blue	Estimate	966	0.08	−0.10	0.53	61
		Lower, upper CL	867, 1055	0.03, 0.13	−8.38, 8.18		
D	Females	Estimate	682	0.14	0.06	0.93 for both sexes combined	1561
		Lower, upper CL	675, 692	0.14, 0.15	0.00, 0.10		
	Males	Estimate	982	0.08	−0.48		132
		Lower, upper CL	952,1013	0.07, 0.09	−1.09, −0.14		

its length and color (see *Results*). The resultant curves for the "females" and "males" fitted the length-at-age data very well (Fig. 4D), as is demonstrated by the high r^2 value of 0.93 for the model fitted to the data that produced the two separate curves (Table 1). Although the L_∞ estimated for the males shown in Fig. 4D was virtually identical to that derived for males in the subset of fish sexed on the basis of their gonadal characteristics in Fig. 4B, the L_∞ for females shown in Fig. 4D was less than that for females whose sex has been determined on the basis of their gonads, reflecting the presence of an increased number of older females and therefore an even greater tendency for the curve to reach an asymptote (Table 1).

The relationship between total length (TL) in mm and total weight (W) in g for *A. gouldii* is $\ln W = 3.041(\ln TL) - 11.017$ ($r^2=0.997$, $P<0.001$, $n=756$) and the relationship between standard length (SL) in mm and total length (TL) in mm is $TL = 1.201 (SL) - 11.883$ ($r^2=0.995$, $P<.001$, $n=101$).

Reproductive biology

Temperatures in inshore and offshore waters at both Albany and Esperance underwent seasonal changes (Fig. 5, A and B). However, they were more pronounced, i.e., peaked earlier in mid-summer vs. early autumn, and reached their minima earlier, i.e., late-winter vs. mid spring, in inshore waters. Furthermore, the differences between water temperatures in inshore waters at the two locations in corresponding months were not as great

as in offshore waters and, in some months, were greater at Esperance than at Albany. Although temperatures in deeper waters at Esperance on the south coast followed essentially the same seasonal trends as those at Albany, they were 1° to 1.5°C lower for each month.

The mean monthly GSIs for female *A. gouldii* ≥ the TL_{50} at maturity, i.e., 653 mm (see later), remained low, i.e., <0.50 between December and May and then rose sharply to a peak of 2.3 in July, before declining to ≤1.6 in August to October and 0.1 in November (Fig. 5C). The gonads of all females collected between November and May with lengths ≥ the TL_{50} at maturity possessed immature and resting ovaries (stage II). Female fish with ovaries at stages III and IV were caught in June and July and those with ovarian stages V and VI, between June and October (Fig. 5C). The above trends in the monthly female GSIs and the prevalence of females at different ovarian stages demonstrate that spawning occurs predominantly between June and October and that females with ovaries that develop beyond stage II will become mature during the spawning period.

The smallest mature female (i.e., with ovaries at one of stages III–VIII) caught during the spawning period measured 391 mm (Fig. 6A). The prevalence of mature females increased from 2% in the 350−399 mm length class to >40% in all length classes above 600 mm, and to 100% in fish >800 mm (Fig. 6A). The estimate for the TL_{50} for female *A. gouldii* at maturity (and its 95% confidence intervals) was 653 mm (623−693 mm).

Figure 5

Mean monthly water temperatures ±1 standard error for (**A**) inshore and (**B**) offshore waters at Albany (gray circles) and Esperance (black circles) on the south coast of Western Australia and (**C**) mean monthly gonadosomatic indices ±1 SE for female western blue groper (*Achoerodus gouldii*) and mean monthly percent frequencies of occurrence of ovaries at stages III and IV (white) and V and VI (gray). Monthly sample sizes are shown on the figure. Closed rectangles on the *x*-axis refer to winter and summer months and the open rectangles to spring and autumn months.

Figure 6

Percent frequency of occurrence of female western blue groper (*Achoerodus gouldii*) with mature gonads (gray histograms) in sequential (**A**) 50-mm length classes and (**B**) five-year age categories in samples obtained during the spawning period, i.e., from June to October. A logistic curve (solid line) and its 95% confidence limits (dotted lines) in (A) were derived from the probability that a fish at a given length is mature. Sample sizes are shown above the histograms for each 50-mm length class and each age category.

The youngest female that was mature during the spawning period was 5 years old. The prevalence of mature females in sequential five-year age categories increased from 7% in fish of 5–9 years to 63% in fish of 20–24 years (Fig. 6B). Although the prevalence of mature females caught during the spawning period reached 81% in fish of 25–29 years, it did not reach 100% in either the 30–34 age-class category or that comprising all older fish (Fig. 6B).
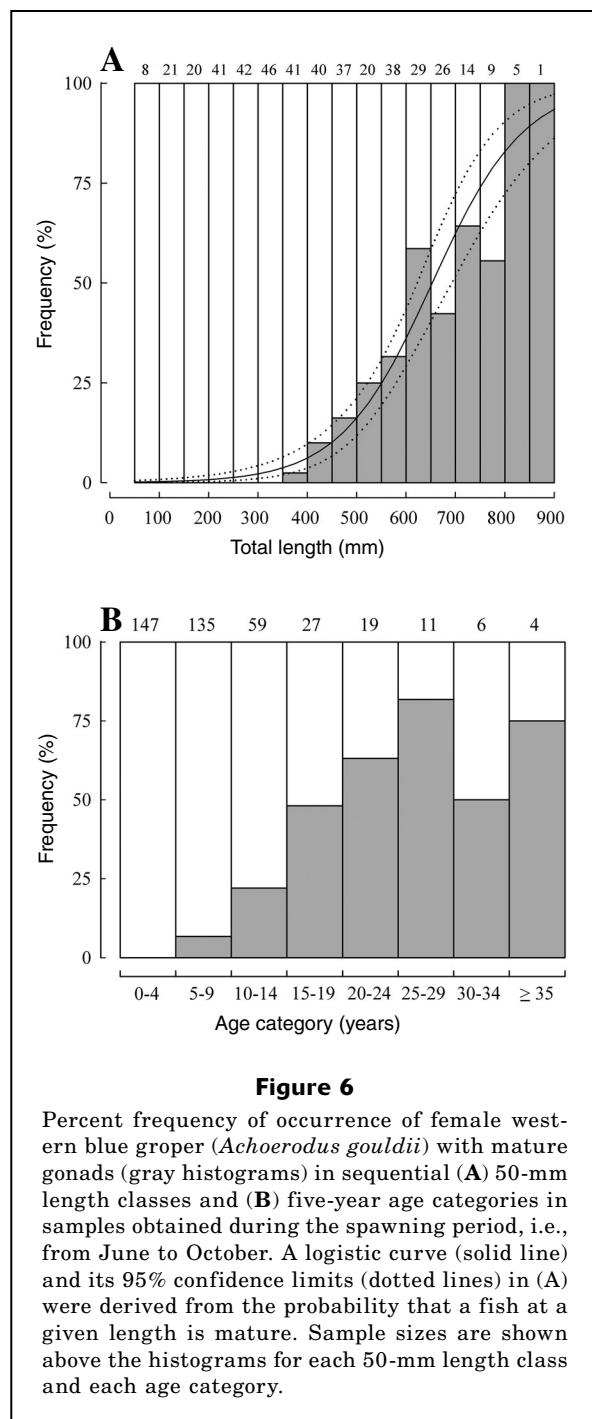
Among the 200 *A. gouldii* with lengths between 100 and 1041 mm and whose gonads were examined histologically, all 150 individuals <655 mm contained exclusively ovarian tissue (Fig. 7A) and were therefore females. All but six of the 50 individuals with lengths ≥655 mm contained exclusively either ovarian tissue (e.g., Fig. 7B) or testicular tissue (e.g., Fig. 7C). The gonadal tissue of those six exceptions—fish whose lengths ranged from 758 to 850 mm—comprised testicular
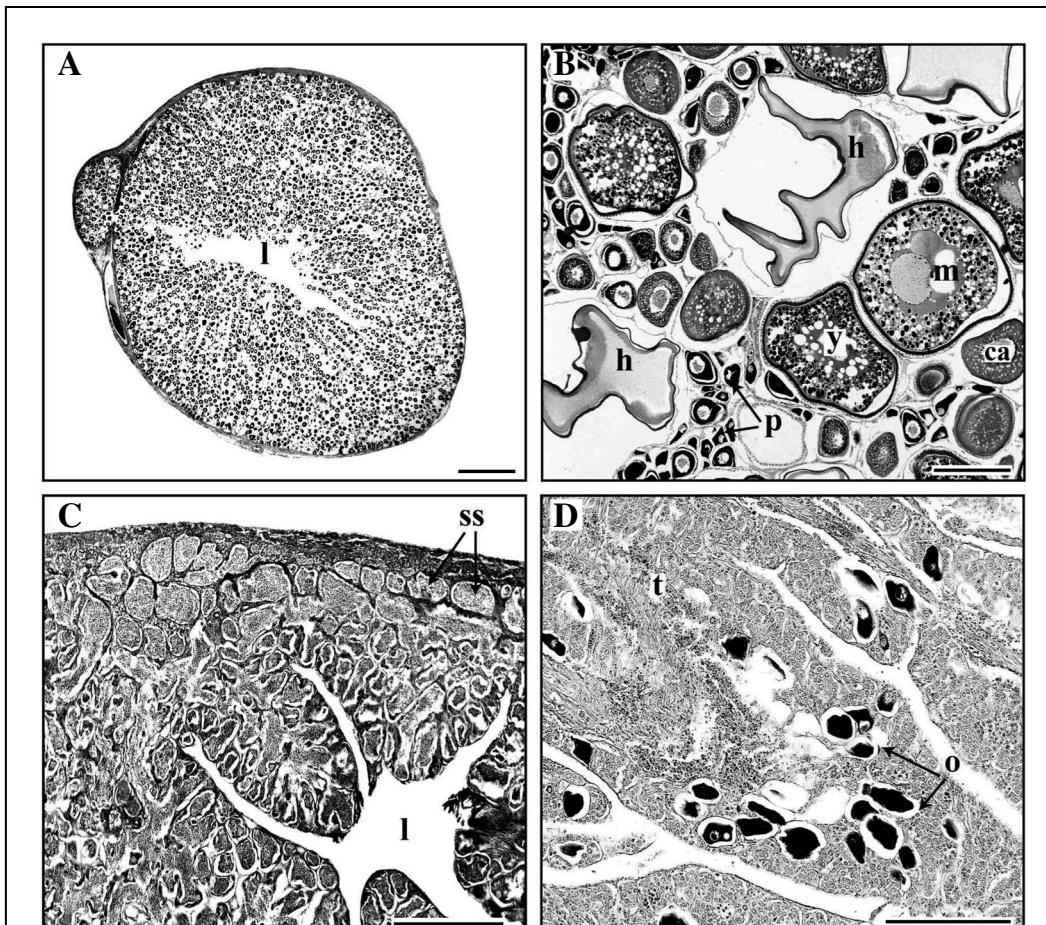
Figure 7

Histological sections of gonads of western blue groper (*Achoerodus gouldii*). (**A**) Ovary of immature female containing numerous previtellogenic oocytes and a prominent lumen (l); (**B**) ovary of mature female containing early previtellogenic oocytes (p), cortical alveolar oocytes (ca), yolk granule oocytes (y), migratory nucleolar oocytes (m), and hydrated oocytes (h); (**C**) mature testes with prominent lumen (l) and sperm sinuses (ss); and (**D**) gonad comprising mainly testicular tissue (t) and numerous previtellogenic oocytes (o). Scale bars = 1000 μm in (A) and 200 μm in (B–D).

tissue within which previtellogenic oocytes were scattered (Fig. 7D).

All immature ovaries, i.e., those containing only previtellogenic oocytes, possessed a prominent central lumen (Fig. 7A). This lumen was largely or fully occluded in mature and spawning ovaries (stages V and VI) (Fig. 7B). A conspicuous central lumen and peripherally located sperm sinuses (Fig. 7D) were present in all mature testes examined histologically.

On the basis of macroscopic examination of all gonads removed from fish and histological examination of a large subsample of those gonads, all *A. gouldii* <655 mm in length were females (Fig. 8A). The prevalence of male fish increased progressively from 3% in the 650–699 mm length class to 80% in the 850–899 mm length class, and to 100% among fish ≥900 mm (Fig. 8A). The TL_{50} at sex change was 821 mm (Table 2).

Among the 891 females, 866 (97%) were green and 39 of the 44 males (89%) were blue. All fish <550 mm were green (Fig. 8B). The prevalence of fish with blue coloration increased rapidly from 8% in the 550–599 mm length class to 86% in the 800–849 mm length class and reached 100% in all fish ≥900 mm (Fig. 8B). The confidence intervals for the TL_{50} of 779 mm at color change overlapped those for the TL_{50} of 821 mm at sex change (Table 2).

All fish <15 years old were females (Fig. 8A). The prevalence of males increased from 9% in fish of 15–19 years to 67% in those of 35–39 years and to 100% in those ≥50 years (Fig. 8A). The trend exhibited by the change from green to blue with increasing age broadly paralleled that for the change from female to male (Fig. 8, A and B). However, a few fish changed color at an even earlier age than the youngest age at which sex change was first found to occur.
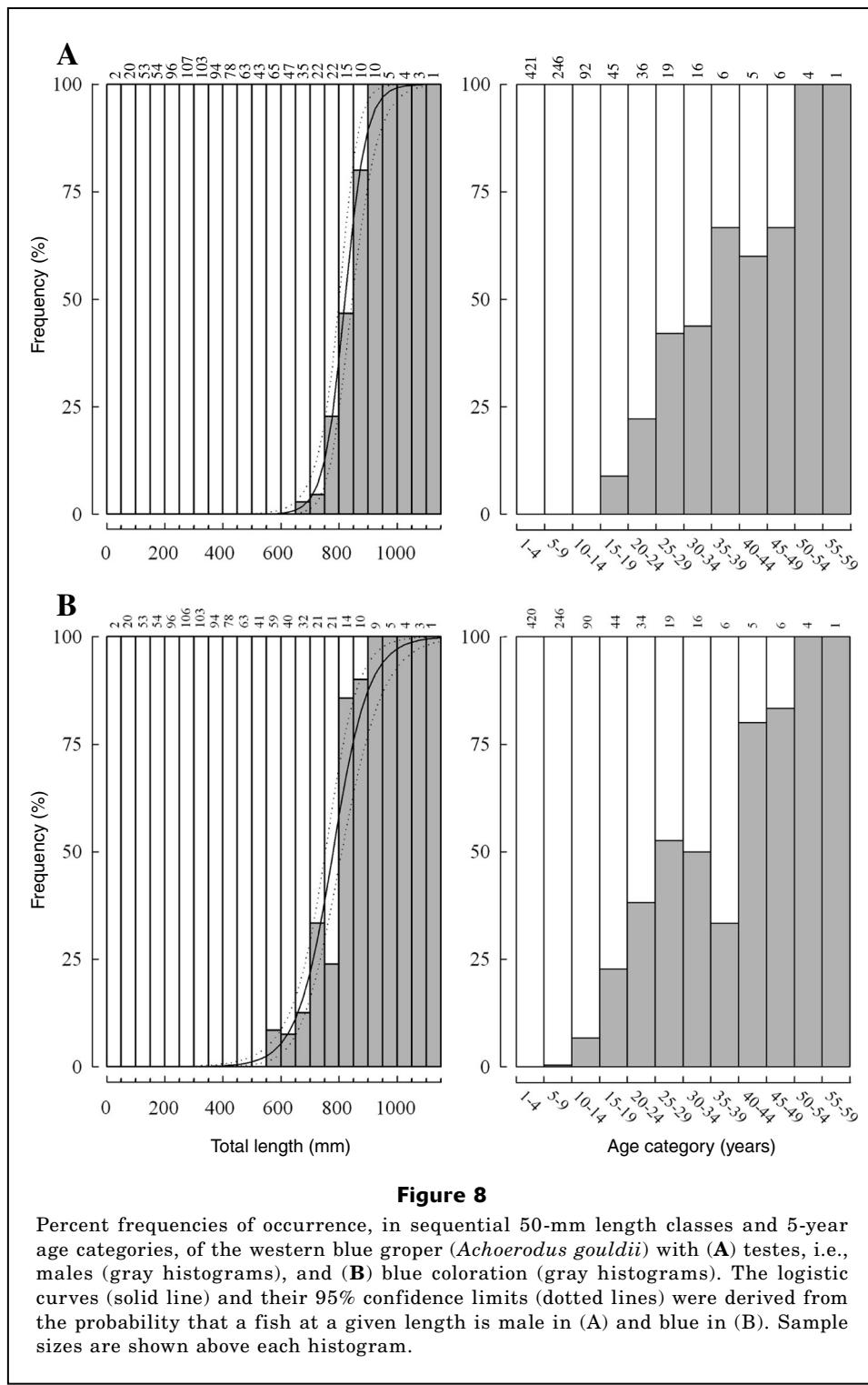
Figure 8

Percent frequencies of occurrence, in sequential 50-mm length classes and 5-year age categories, of the western blue groper (*Achoerodus gouldii*) with (**A**) testes, i.e., males (gray histograms), and (**B**) blue coloration (gray histograms). The logistic curves (solid line) and their 95% confidence limits (dotted lines) were derived from the probability that a fish at a given length is male in (A) and blue in (B). Sample sizes are shown above each histogram.

The values for the AIC showed that the dichotomous factor, color, is not as good a predictor as the continuous variable, length, that an individual is male (Table 3). However, the likelihood-ratio test demonstrated that the combination of color and length provided a significantly better fit than length alone (*P*=0.012).

Recruitment variability, mortality, and spawning potential ratio

From the data shown in Figure 3, it is assumed that *A. gouldii* becomes fully recruited to the commercial gillnet fishery by 15 years of age. Because a substantial

number of fish >35 years old were caught by this fishery and the distribution of the lengths of the males did not appear to be truncated, mesh selectivity did not apparently exert a major influence on the upper end of the length distribution.

Relative abundance analysis demonstrated that, in the three successive 12-month periods between August and July, 11 of the year classes between 1936 and 1992 differed significantly from the average level of recruitment. The strengths of the 1972, 1980, 1983, and 1990 year classes were 3.6, 2.6, 2.1, and 1.5 times greater, respectively, than the average level of recruitment (Fig. 9). Among the other year classes that differed significantly from the average level of annual recruitment, the 1981, 1958, 1971, and 1944 year classes were strong, whereas the 1991, 1992, and 1985 year classes were weak (Fig. 9).

The total mortality estimate, Z, of 0.086/year (0.08–0.092/year), derived from the catch curve analysis with the assumption of constant recruitment, was slightly less than the 0.093/year (0.08–0.092/year), derived for Z by using the relative abundance analysis and assuming variable recruitment. The estimate for M, derived by refitting Hoenig's (1983) equation for fish and inserting the maximum age for *A. gouldii*, was 0.072/year (0.022–0.180/year). The approach of Hall et al. (2004), which was used to refine the above estimate of M, yielded a lower value, i.e., 0.054/year (0.021–0.090/year). Fishing mortality, F, was estimated to be 0.039/year (0.003–0.073/year).

The spawning potential ratio at the current estimated level of F, on the basis of spawning stock biomass per recruit and calculated by using the von Bertalanffy growth curves for the females and males of *A. gouldii* shown in Figure 4D, was 0.88 (0.75–0.99) for females and 0.52 (0.27–0.96) for males (Fig. 10).

Discussion

Demonstration of protogynous hermaphroditism

Our histological examination of the gonads of a large number of fish from throughout the year and covering a wide size range of *A. gouldii* fulfils one of the important requirements for demonstrating, with certainty, that a fish species is a functional hermaphrodite (Sadovy and Shapiro, 1987). Because all of the numerous *A. gouldii* captured with lengths of 100 to 655 mm were females and the prevalence of males subsequently rose with increasing body size to the extent where they constituted 100% of the larger fish, all males of *A. gouldii* are apparently derived from females. This conclusion is supported by the fact that all of the 164 individuals <15 years old, and whose gonads were examined histologically, were shown to be females. Moreover, the proportion of males subsequently increased progressively with age to the point where over 50% of individuals ≥35–39 years old were males. Because the length at which the prevalence of males reached 50% of fish (821 mm) was substantially greater than the TL_{50} at

Table 2

Estimates of the total lengths (and their lower and upper 95% confidence limits [CLs], in mm) at which 50% (TL_{50}) and 95% (TL_{95}) of western blue groper (*Achoerodus gouldii*) change sex to male and the total lengths at which 50% and 95% of *A. gouldii* change from green (females) to blue (males) in southwestern Australia.

		TL_{50}	TL_{95}
Sex change	Estimate	821	930
	Lower CL	800	890
	Upper CL	845	1102
Color change	Estimate	779	961
	Lower CL	753	910
	Upper CL	809	1028

Table 3

Results of logistic regression analysis for determining whether color or total length (TL, in mm), or color and total length combined, were the best predictors of whether an individual of western blue groper (*Achoerodus gouldii*) was male. LL = log-likelihood; α, β_1, β_2 are constants; AIC = Akaike's information criterion.

Parameter	Color	TL	Color and TL
LL	−84.424	−48.644	−45.457
α	−4.631	−17.275	−15.505
β_1		0.021	0.018
β_2	4.979		1.477
AIC	172.847	101.289	96.913

maturity (653 mm) for females and greater than that at which all female fish were apparently destined to become mature, a large number of male *A. gouldii* must have been derived from mature females. Thus, the characteristics of *A. gouldii* fulfil the criteria of Sadovy de Mitcheson and Liu (2008) for designating this species as a protogynous hermaphrodite. Although, on their own, these features do not provide concrete evidence that *A. gouldii* is monandric, i.e., all males are derived from mature females (Sadovy de Mitcheson and Liu, 2008), they do raise the strong possibility that this is the case for this labrid. As with other protogynous labrids (e.g., Reinboth, 1970; Sadovy and Shapiro, 1987), the presence of a central lumen in all mature testes of *A. gouldii* is considered to represent the retention of the ovarian lumen and to account for the peripheral location of the sperm ducts in those testes.

Aging methods, length and age compositions, and growth patterns

Although the von Bertalanffy growth curve provided a good fit to the lengths at age for all aged individuals
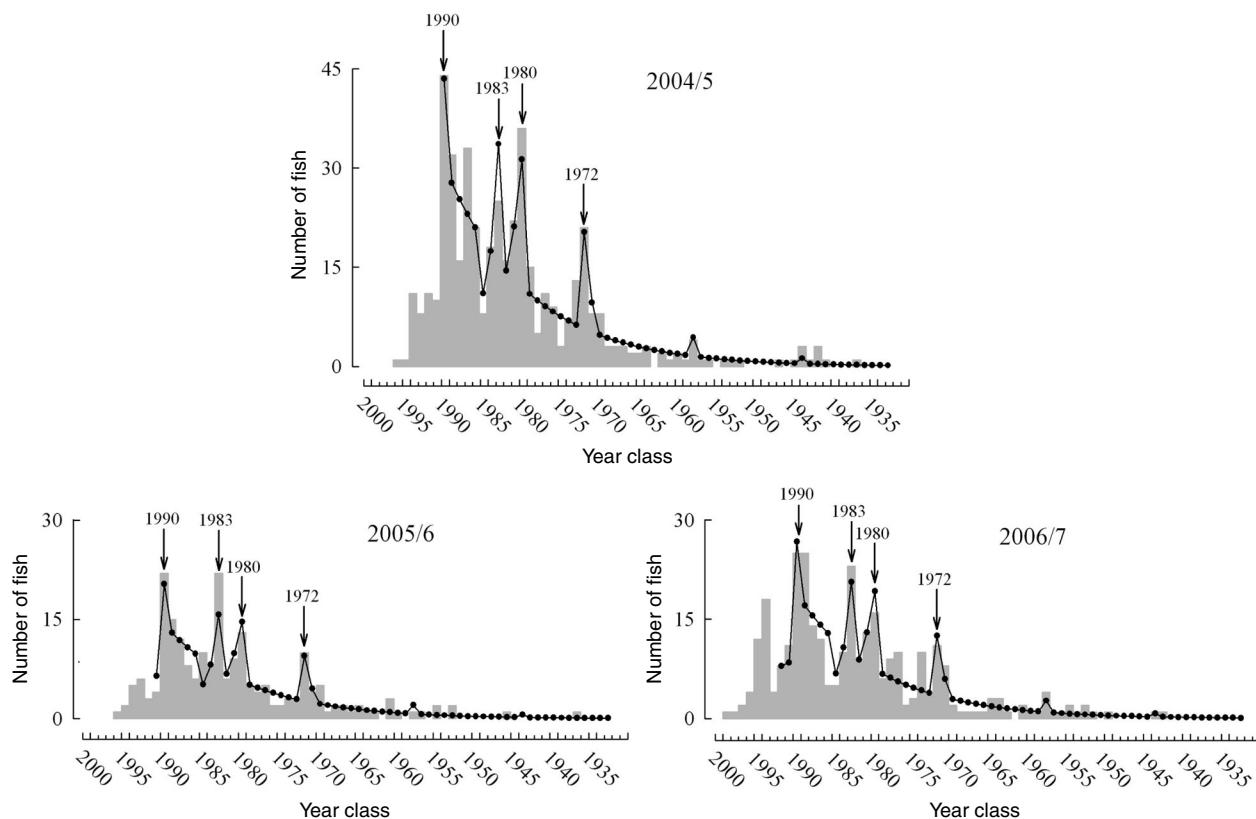
Figure 9

Observed numbers of individuals of each year class of western blue groper (*Achoerodus gouldii*) in commercial gillnet samples obtained from the south coast of Western Australia between August and July in 2004–5, 2005–6, and 2006–7 (histograms). Dotted lines represent the expected numbers of fish of each year class, as determined from a relative abundance analysis and were fitted to the observed frequency of abundance of fish in each year class in each of the three 12-month periods. Variable recruitment was assumed for creating the dotted lines; 1972, 1980, 1983, and 1990 (denoted with arrows) were years of particularly strong recruitment.
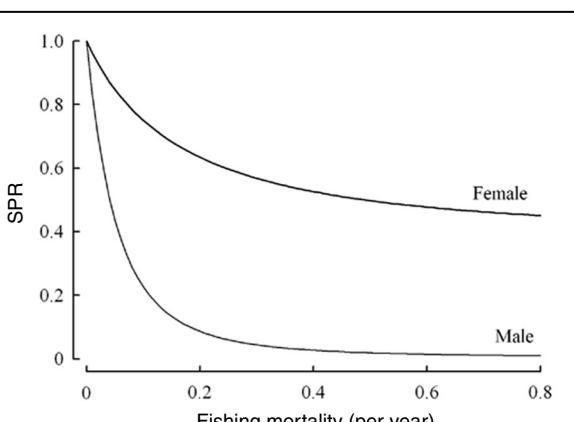
Figure 10

The effect of fishing mortality (*F*) on the spawning potential ratio (SPR) for females and males of the western blue groper (*Achoerodus gouldii*), calculated by using the age of 15 years (the age currently calculated to represent full recruitment into the commercial gillnet fishery).

of *A. gouldii*, irrespective of their sex, the variation in the lengths at age became very marked after ~25 years (Fig. 4A). This variation reflects a marked upward divergence in the growth of males from that of females among the larger and older fish (Fig. 4B). The fact that the von Bertalanffy growth parameters for green and blue fish were very similar to those derived for females and males, respectively, in data for the same subset of individuals, demonstrates that growth curves based on color provide a good proxy for those based on sex alone (Fig. 4, B and C).

A substantial number of the larger and older fish obtained during the study had been eviscerated before we collected them and therefore sex could not be determined and used to provide length-at-age data for constructing growth curves for the two sexes. Consequently, some caution must be exercised in drawing conclusions for the upper end of the growth curves constructed using fish of known sex, or for the same fish after separation by color. The AIC test used on the above subsample demonstrated that a combination of length and color provided a better indication of the sex

of a fish than either of those variables on their own. Although sex was determined for only a proportion of the large fish, the length and color of all fish were recorded. This enabled us to construct growth curves for females and males that incorporated the length at age for each individual of unknown sex, allowing for the probability that, from its length and color, it would be of a particular sex. Through increasing substantially the numbers of large fish from those whose sex was just determined from their gonads, the von Bertalanffy growth curves thereby derived for females and males are considered to provide better representations of the growth throughout life of the two sexes of *A. gouldii* than those derived solely from fish whose sex was unknown.

The greater length of males than females of *A. gouldii* at corresponding ages parallels the situation recorded for a number of other protogynous fishes, e.g., the cylindrical sandperch (*Parapercis cylindrica*), the heavybeaked parrotfish (*Chlorurus gibbus*), the greenfin parrotfish (*Chlorurus sordidus*), the swarthy parrotfish (*Scarus niger*), and the sixband parrotfish (*Scarus frenatus*) (Choat et al., 2006; Munday et al., 2004; Walker and McCormick, 2004), as well as its congener *Achoerodus viridis* (Gillanders, 1995a). Comparisons of the distributions of the lengths at age of the two sexes (Fig. 4B) strongly indicate that the fastest growing *A. gouldii* have the greatest tendency to change from female to male, a conclusion which parallels that drawn by Munday et al. (2004) for the labrid *S. frenatus*. However, some of the oldest fish were females (Fig. 4, B and D) and therefore some female *A. gouldii* were apparently not destined to become males, as is also the case with *Cheilinus undulatus* (Choat et al., 2006).

As hypothesized, the greater TL attained by *A. gouldii* (1162 mm) than by *A. viridis* (773 mm, after conversion from the SL given by Gillanders, 1995a), corresponded to a greater maximum age of 70 years for *A. gouldii* in comparison to 35 years for *A. viridis*. The maximum age of the large temperate *A. gouldii* is thus twice that estimated by Gillanders (1995a) for *A. viridis*, and by far the greatest yet recorded for any species of labrid, including the large tropical species *C. undulatus*, which attains a maximum age of 32 years (Choat and Bellwood, 1994; Choat et al., 2006). Although Hostetter and Munroe (1993) concluded that other large temperate labrids have long life spans, Choat et al. (2006) considered that the life spans of the large labrids that they used to make this generalization, typically <30 years of age, are relatively short. In the context of *A. gouldii*, the exceptional age attained by males was accompanied by a marked tendency for growth to an asymptote, which is not typically the case with the males of large tropical labrids (Choat et al., 2006).

Reproductive biology

The vast majority of the *A. gouldii* caught by spear fishing at numerous sites in nearshore waters were obtained from over the granite reefs that dominate the hard-structured substrate found in those waters along the south coast of Western Australia, and around the islands off the coast (Kendrick, 1999; Sanderson et al., 2000). Because the sizes of these fish, which were representative of the *A. gouldii* observed in those clear waters, were predominantly <600 mm and <12 years old, and therefore below the TL_{50} at maturity, the reef areas in nearshore waters constitute an important nursery habitat for juvenile *A. gouldii*. Large numbers of *A. gouldii* >500 mm, many of which were mature during the spawning season, were caught in deeper waters and this finding indicates that the individuals of this species move offshore as they increase in body size and become mature. This movement and the spawning of *A. gouldii* in offshore, deeper waters are consistent with the conclusions drawn by Shepherd and Brook (2007) for this species.

Our data indicate that, on the south coast of Western Australia, *A. gouldii* spawns in offshore waters between early winter and mid-spring, when water temperatures are declining to their minima (Fig. 5B); the preference for offshore waters and an early winter to mid-spring season for spawning parallels the situation with the congeneric *A. viridis* in eastern Australia (Gillanders, 1995a). Although there are no data on the larval phase of *A. gouldii*, Leis and Hay (2004) have shown that the larvae of *A. viridis* settle at 7–8 mm, metamorphose into juveniles by about 10 mm, and have hypothesized that the larvae of this species have some behavioral control over their movement from the shelf to their nearshore nursery habitats. Consequently, it is proposed that the spawning of *A. gouldii* in winter enables the larvae of this species to recruit into protected, nearshore coastal waters, at a time when the temperature and productivity in those waters have already started to increase (Fig. 5A) and winds are at their weakest and thus collectively provide an optimum environment for early juvenile growth.

The hypothesis that the greater length and age attained by *A. gouldii* than by *A. viridis* is accompanied by a greater length and age at maturity of females was confirmed by our results. With *A. gouldii*, the smallest mature female was 391 mm and the TL_{50} of females at maturity was as high as 653 mm. Furthermore, only one of the 164 females <5 years old was mature, and maturity was not attained by ~50% of females until they had reached 15–19 years in age. Although Gillanders (1995a) did not estimate the TL_{50} at maturity for female *A. viridis*, she recorded that females first matured at 200–220 mm SL (=246–270 mm TL) and that the majority had become mature by 240–280 mm SL (=294–341 mm TL). Gillanders (1995a) also found that, although a few female *A. viridis* became mature at the end of their second year of life, the majority matured between their third and fifth years of life. As with maturity, sex change occurred at a greater length and age in *A. gouldii* than in the smaller *A. viridis*. Thus, whereas sex change commenced in *A. gouldii* at ~650 mm and 15 years of age, and the TL_{50} at sex change was as high as 821 mm (TL), it began in *A. viridis* at lengths of ~600 mm (500 mm SL) and as early as 10 years of age (Gillanders 1995a).

Achoerdus gouldii undergoes the type of color change that is broadly associated with sex change in most protogynous labrids (e.g., Roede, 1972; Gillanders, 1995a; McBride and Johnson, 2007) and which, in *A. gouldii*, involves a shift from green to blue rather than from reddish brown to blue as in *A. viridis* (Gillanders, 1999). However, as with the latter congeneric species, some females (3%) were not of the initial color and some of the males (11%) did not have the terminal color. Furthermore, the continuous variable, length, was found to be a better predictor of sex than the dichotomous variable, color; however, a combination of both of these variables further improved one's ability to predict the sex of individuals of *A. gouldii*. The fitting of logistic curves to the length data for fish with testes and with blue coloration yielded TL_{50}s of 821 and 779 mm, respectively. Although these two TL_{50}s differed by 42 mm, their 95% confidence limits overlapped and therefore color can be used to derive an approximate value for the TL_{50} at sex change when it is not possible to record the sex of individuals because, for example, their viscera had been removed or fish were being viewed live during visual surveys. Our approaches to using color as a proxy for sex for estimating the TL_{50} at sex change and for enhancing the description of the growth of females and males are likely to be applicable to many of the numerous species that exhibit a similar form of sexual dichromatism.

Recruitment variability, mortality, and spawning potential ratio

The pattern of flow of the Leeuwin Current, the predominant current on the southwest coast of Australia in winter and therefore during the spawning period of *A. gouldii*, leads to the larvae of certain teleosts and the western rock lobster (*Panulirus cygnus*) being dispersed offshore (Pearce and Phillips, 1988; Gaughan, 2007). Thus, because *A. gouldii* is recruited into nearshore waters, it appears relevant that this species exhibited particularly strong recruitment in 1972, 1980, 1983, and 1990, when the Leeuwin Current was weak (Pearce and Phillips, 1988; Caputi et al., 1996), and very poor recruitment in 1991 and 1992 when the Leeuwin Current was especially strong.

Because the current level of fishing mortality for *A. gouldii* in southwestern Australian waters is estimated to be 74% of natural mortality, this species is apparently close to or at full exploitation in these waters (after applying a reference point $F_{lim} = \frac{2}{3} M$ based on Patterson [1992]). The conclusion that *A. gouldii* is close to or at full exploitation is consistent with the estimate for the spawning potential ratio (SPR) for the males of this protogynous hermaphroditic labrid. This value has therefore declined to 0.52 and, given the steepness of the curve relating SPR to fishing mortality, is rapidly approaching 0.30, which is often regarded as the level at which a stock is considered to be overfished (Goodyear, 1993; Mace and Sissenwine, 1993). Indeed, the lower 95% CL of 0.27 for the SPR lies below this reference point.

Implications for management

Most recreational line and spear fishing for *A. gouldii* on the south coast of Western Australia occurs in shallow and relatively accessible waters, where the individuals of this species are typically smaller than those in deeper waters and where most individuals are less than the TL_{50} of 653 mm at which females attain maturity. Furthermore, in deeper waters, 52% of the *A. gouldii* taken by the commercial fishery were less than the length at maturity and 88% were below the TL_{50} of 821 mm at which females change sex to males. Moreover, *A. gouldii* often suffers barotrauma when brought to the surface from particularly deep waters, as is the case with many other demersal species in Western Australia and elsewhere (e.g., St John and Syers, 2005; Parker et al., 2006), and with other labrids (e.g., Nardi et al., 2006). Thus, if the current minimum legal length of 500 mm is maintained, or slot (minimum and maximum length) limits are introduced, fishing crews should be encouraged to adopt fishing practices that minimize the loss of released fish. In this context, it would be of great value to undertake research into the effects of barotrauma on *A. gouldii* and the ways in which the loss of released fish may be minimized.

Although substantial fishing of protogynous species can lead to a marked decline in the relative abundance of their males (e.g., Coleman et al., 2000), the size at sex change of some protogynous species declines in response to the selective removal of large males by fishing (e.g., Platten et al., 2002; Hawkins and Roberts, 2003). Because it is not known whether the size at sex change of *A. gouldii* is labile, it would be prudent for managers to take the conservative view that this is not necessarily the case with this labrid.

Because fisheries for protogynous species, such as *A. gouldii,* have a greater effect on the spawning biomass of males than females, managers need to take into account the potential for fishing to lead to sperm limitation, reduced fertilization success, and social or behavioral changes, and to consider whether appropriate biological reference points need to be established to ensure that the sex and size structure of the fish stock is maintained (Alonzo and Mangel, 2004, 2005; Brookes et al., 2008). Because it would be useful for managers to have a rapid and inexpensive means for determining the sex of individuals of *A. gouldii*, our data are relevant in that they show that body color can be used as a broad surrogate for sex and it would enable rapid monitoring of the population to detect whether changes are occurring in the ratio of the biomasses of mature females and males and in the length at sex change, both of which could be used as the basis for an appropriate fishery control rule. In our estimates of the effect of increased fishing mortality on male spawning biomass per recruit, we did not assume that compensatory phenotypic or behavioral responses of the types explored by Alonzo and Mangel (2005) occurred in the pattern of sex change of *A. gouldii*. Consequently, our results provide a precaution-

ary evaluation of the implications of increased fishing mortality on the males.

Beamish et al. (2006) have recently drawn attention to the importance, when considering long-lived species, of understanding the effects of removing large numbers of the older age classes, which they referred to as longevity overfishing. In this context, managers need to recognize that our age-frequency distributions indicate that commercial gill netting captures the older age classes of *A. gouldii*. It is instructive to consider the potential for overfishing of the very long-lived (maximum age, 70 years) *A. gouldii* in the context of the response to heavy fishing by the smaller and earlier maturing but still quite large and relatively long-lived congener *A. viridis* (maximum age, 35 years). *Achoerodus viridis* suffered such heavy fishing mortality in eastern Australia that the waters of that region were closed to commercial and recreational fishing for that species and still remain closed to spear and commercial fishing (Gillanders, 1999).

When assessing which combination of typical fishery controls should be applied to *A. gouldii*, e.g., possession limits, controls on fishing gear or effort, minimum or maximum (fish) size limits (or both), and closed areas and seasons, consideration needs to be given to the effects of the various controls on both the commercial and recreational fishing sectors and the likely effectiveness of each control in helping to restore or maintain the reproductive potential of both the females and males of this species. In particular, managers should recognize that the inshore recreational fishery is a multispecies fishery, which, for *A. gouldii*, is a gauntlet fishery (i.e. a fishery largely restricted to catching fish of a limited period of their life cycle) that catches mainly smaller individuals. In contrast, the commercial fishery, which operates in deeper, offshore waters and targets elasmobranchs and a mix of other teleost species as well as *A. gouldii*, catches larger and older individuals of that species. Because the catches of the commercial fishery are buffered by the presence of a greater number of age classes than the recreational fishery, the commercial catches are less likely to experience the effects of recruitment variability. The use of a single control is therefore likely to have more effect on one fishing sector than the other. The strategies developed for managing *A. gouldii* in the future will need to balance the ways in which they affect the different fishing sectors. Furthermore, if fishing crews are to accept management controls, they will need to be informed of the implications of the particular biological characteristics of *A. gouldii* for the fishery and the effects of catches by different fishing sectors on the stocks of this species.

In summary, we have shown that the temperate *A. gouldii* is long lived (maximum age, 70 years), relatively slow growing and late maturing (~17 years)—characteristics that contrast with the those typically found in labrids, most of which are tropical. However, these characteristics are found with many large epinephelines (e.g., Morris et al., 2000) and numerous deep-water species (e.g., Koslow et al., 2000; Morato et al., 2006;

Marriott et al., 2007), and they make these species particularly susceptible to overfishing. The variable recruitment of *A. gouldii* would also be likely to increase the susceptibility of this species to overfishing, as it does with other species (e.g., Koslow et al., 2000; Sadovy, 2001; Hawkins and Roberts, 2003). Furthermore, because *A. gouldii* does not typically change sex until a relatively old age (35–39 years), the abundance of the males of this protogynous hermaphrodite would be especially at risk of becoming depleted through fishing. The results of this study emphasize the need to acquire a thorough understanding of the life cycle characteristics of species that will almost inevitably become increasingly exploited in the future and, as Coleman et al. (2000) pointed out for reef fishes in North America, and not interpret a lack of such information as representing the absence of a potential problem.

Acknowledgments

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