

Abstract—Samples of the commercially and recreationally important West Australian dhufish (*Glaucosoma hebraicum*) were obtained from the lower west coast of Australia by a variety of methods. Fish <300 mm TL were caught over flat, hard substrata and low-lying limestone reefs, whereas larger fish were caught over larger limestone and coral reef formations. Maximum total lengths, weights, and ages were 981 mm, 15.3 kg, and 39 years, respectively, for females and 1120 mm, 23.2 kg, and 41 years, respectively, for males. The von Bertalanffy growth curves for females and males were significantly different. The values for L_{∞} , k , and t_0 in the von Bertalanffy growth equations were 929 mm, 0.111/year, and -0.141 years, respectively, for females, and 1025 mm, 0.111/year, and -0.052 years, respectively, for males. Preliminary estimates of total mortality indicated that *G. hebraicum* is now subjected to a level of fishing pressure that must be of concern to fishery managers. *Glaucosoma hebraicum*, which spawns between November and April and predominantly between December and March, breeds at a wide range of depths and is a multiple spawner. The L_{50} 's for females and males at first maturity, i.e. 301 and 320 mm, respectively, were attained by about the end of the third year of life and are well below the minimum legal length (MLL) of 500 mm. Because females and males did not reach the MLL until the end of their seventh and sixth years of life, respectively, they would have had, on average, the opportunity of spawning during four and three spawning seasons, respectively, before they reached the MLL. However, because *G. hebraicum* caught in water depths >40 m typically die upon release, a MLL is of limited use for conserving this species. Alternative approaches, such as restricting fishing activity in highly fished areas, reducing daily bag limits for recreational fishermen, introducing quotas or revising specific details of certain commercial hand-line licences (or doing both) are more likely to provide effective conservation measures.

Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species

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The West Australian dhufish (*Glaucosoma hebraicum*), also known as the Westralian jewfish (McKay, 1997), is one of the most commercially valuable and recreationally sought after finfish in Western Australia (Sudmeyer et al.¹). This species is confined to southwestern Australia, where its distribution ranges southwards from Shark Bay at 26°00'S, 113°00'E down the west coast and then eastwards along the south coast to the Recherche Archipelago at 34°10'S, 122°15'E (Hutchins and Thompson, 1995). *Glaucosoma hebraicum* is one of four members of the monogeneric family Glaucosomatidae, which also includes the pearl perch (*Glaucosoma scapulare*) that is fished commercially and recreationally in eastern Australia (McKay, 1997).

Despite the high quality of the flesh of *Glaucosoma* species and the commercial and recreational importance of *G. hebraicum* in particular, there are no refereed papers on the biology of any species in this genus. Furthermore, the results of undergraduate studies on the biology of *G. hebraicum*, which were collated by Sudmeyer et al.,¹ included estimates of age that were based on the number of growth zones in whole otoliths, an approach that would almost certainly have underestimated the age of many older fish (see "Results" section).

Numerous commercial and recreational fishermen report that they now fish much farther offshore in order to obtain catches of dhufish comparable with those they had previously been

able to obtain from nearer the coast. This consistent circumstantial evidence strongly suggests that the abundance of *G. hebraicum* in more inshore waters has declined in recent years and that this is particularly the case in areas near the city of Perth where this species has been targeted by recreational fishing crews. The indications that the abundance of dhufish in nearshore waters was declining led the Australian Fisheries Research and Development Corporation to fund the current study, with a view to producing biological data for managing *G. hebraicum*.

During the present study, we first determined whether the otoliths of *G. hebraicum* had to be sectioned to detect all of their opaque zones and we then validated that these opaque zones are formed annually and could thus be used to age this species. As accurate estimates of the age of a fish are dependent on a reliable birth date, the trends exhibited by reproductive variables were used to estimate the duration of the spawning period and, in particular, when spawning activity peaked. The age of each fish was then determined and the resulting length-at-age

¹ Sudmeyer, J. E., D. A. Hancock, and R. C. J. Lenanton. 1992. Synopsis of Westralian jewfish (*Glaucosoma hebraicum*) (Richardson, 1845) (Pisces: Glaucosomatidae). Fisheries Research Report 96, Western Australian Marine Research Laboratory, Fisheries Western Australia, PO Box 20, North Beach 6020, Western Australia.

data employed to determine the age compositions and growth rates of female and male *G. hebraicum*. The reproductive variables were also used to help ascertain where *G. hebraicum* spawns and whether this species is a multiple spawner *sensu* deVlaming (1983), i.e. whether individual females release eggs on more than one occasion in a spawning season. The lengths of both sexes at first maturity were calculated to determine whether they lay below the minimum legal length (MLL) of 500 mm and were thus appropriate for helping to conserve this species. The ages at which females and males mature were also determined in order to elucidate whether fish might spawn in one or more spawning seasons before they attain the MLL. Attempts were also made to ascertain the types of habitat occupied by *G. hebraicum* at different stages during its life cycle and to obtain preliminary mortality estimates which could be used as an indicator of whether this species is being lightly or heavily fished. Finally, the data collected during this study were used to discuss ways in which the fishery for *G. hebraicum* might be managed most appropriately in the future.

Materials and methods

Glaucosoma hebraicum, that were less than the MLL of 500 mm total length (TL), were collected between May 1996 and June 1999 by commercial trawls, hand-lines, and a recreational spear diver under a research collection permit issued by Fisheries Western Australia—the government agency responsible for managing the fishery for this species. Filleted carcasses of *G. hebraicum* ≥ 500 mm TL, together with their gonads, were obtained monthly between May 1996 and April 1998 from commercial fish-processing plants and weigh-ins at local recreational fishing club competitions. These fish had been caught by commercial or recreational rod and hand-lines along the lower west coast of Australia between Mandurah (32°32'S) and the Houtman Abroholos (28°35'S), i.e. within that part of the distribution of *G. hebraicum* where this species is considered to be most abundant and is most heavily fished.

The total length of each fish was measured to the nearest 1 mm and the weight of each fish < 500 mm was weighed to the nearest 1 g. The weights of 334 females and 442 males ≥ 500 mm TL were weighed to the nearest 10 g prior to filleting. The relationship between total length (L) in mm and total wet weight (W) in g of each sex was

$$\begin{aligned} \text{Females} \quad \log W &= \log 0.0000417 + 2.859 \log L \\ &\quad (n=486, r^2=0.995) \\ \text{Males} \quad \log W &= \log 0.0000322 + 2.898 \log L \\ &\quad (n=572, r^2=0.995). \end{aligned}$$

These relationships were then used to estimate the weights of the female and male fish that had been filleted but not weighed. Note that all of the logarithm values recorded in this paper are natural logarithms.

On several occasions, a video camera, attached by cable to a television monitor and video recorder, was lowered

over the substrata during commercial hand-line fishing for dhufish. Video footage of the substrate over which dhufish were caught was later examined to determine the types of habitat occupied by this species.

Age determination

The two sagittal otoliths of each fish were removed, cleaned, dried, and then stored in paper envelopes. All sagittal otoliths were sectioned, except for those which, when placed in methyl salicylate and examined microscopically under reflected light against a black background, could clearly be seen to possess either no opaque zones or only a single opaque zone. However, because the opaque zones in the whole otoliths of large fish were so numerous and closely spaced that they were often difficult to distinguish from one another and because previous estimates of the age of dhufish were based on counts of opaque zones in whole otoliths (Sudmeyer et al.¹), the number of opaque zones visible in 100 otoliths, obtained from a wide size range of fish, were compared prior to and after sectioning to ascertain whether sectioning increased one's ability to detect the opaque zones.

For sectioning, the otoliths were mounted in clear epoxy resin and cut into 500 μm sections with a low-speed diamond saw (Buehler). The sections were cleaned and mounted on slides with DePX mounting medium and examined under reflected light with a dissecting microscope attached to a video camera (Panasonic WV-CD20). The image was analyzed by using the computer imaging package Optimas 5 (Optimas, 1995). The number of opaque zones in each otolith was always counted twice and on different days and without knowledge of either the date of capture or the size of the fish from which the otolith came, and also, in those cases where the two counts differed, on a third occasion. Although the number of times that a third count did not agree with either of the two previous counts was negligible for otoliths with less than 15 opaque zones, such disagreement increased to ca. 10% for otoliths with 15–25 opaque zones and ca. 30% for those with more than 25 opaque zones. When a third count was necessary and was not the same as either of the two previous counts, further counts were made until successive counts did not differ by more than two opaque zones. On such occasions, the final count was recorded.

An independent reader counted the number of opaque zones on 110 otoliths from a wide size range of fish. Eighty four percent of the counts of the number of opaque zones made by this independent reader were the same as those of the senior author for 50 sectioned otoliths that had been judged by the senior author to have up to 10 such zones and, in those cases where there were discrepancies, the differences were never more than one opaque zone. Eighty percent of the counts made by the independent reader of the number of opaque zones on 50 sectioned otoliths recorded as possessing between 11 and 25 such zones by the senior author were the same or differed by only one from those of the senior author and, where there were discrepancies, these rarely exceeded three opaque zones. In the case of ten otoliths with > 25 opaque zones, the maximum dis-

crepancy between the counts recorded by the independent reader and the senior author was five. After consultation, it was agreed that, in many of the cases where the counts differed by one opaque zone, the independent reader had failed to discern the outermost opaque zone at the periphery of the otoliths. Moreover, the extent of any discrepancy between the counts of the independent reader and the senior author declined if the independent reader continued to recount the number of opaque zones on the otoliths.

Validation that the opaque zones in the otoliths of *G. hebraicum* are formed annually was carried out by analyzing the trends exhibited throughout the year by the marginal increments on whole otoliths, when only one opaque zone was present, and on sectioned otoliths when two or more opaque zones were present. For this purpose, the marginal increment on each otolith, i.e. the distance between the outer edge of the single or outermost opaque zone and the edge of the otolith, was expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. Each of the above requisite distances was measured perpendicular to the opaque zone(s) and without knowledge of the date of capture of the fish and was recorded to the nearest 0.01 mm by using Optimas 5. The values for the marginal increments were separated into groups according to the number of opaque zones on the otoliths, i.e. 1, 2–5, 6–8, 9–11 etc., after which the values for each of those groups in each corresponding month of the year between May 1996 and April 1998 were pooled.

Von Bertalanffy growth equations

The time when spawning peaked was estimated from the trends exhibited throughout the year by gonadosomatic indices, gonadal maturity stages, and pattern of oocyte development. This time was considered to correspond to the birth date of *G. hebraicum* and could thus be used, in combination with the number of opaque zones on the otolith and the time when the annulus becomes delineated on the otolith, to determine the age of individual fish on their date of capture. Because the sex of fish <150 mm could not be determined, the lengths-at-age of these small fish were randomly allocated in equal numbers to the data sets for female and male fish used for constructing the growth curves.

Assumptions are made concerning the distribution of errors when fitting von Bertalanffy growth curves to length-at-age data. Kimura (1980) discussed the implications of the following three assumptions, namely that 1) the individual lengths-at-age have a constant variance, 2) the mean lengths-at-age have a constant variance and 3) the variance of the lengths-at-age is dependent on age. The assumption most frequently adopted in growth studies is that the individual lengths-at-age have a constant variance. As discussed by Kimura (1980), different assumptions regarding the error variance require modifications to the objective function to ensure that the parameters are estimated accurately and that any comparisons between growth curves, that are based on the likelihood ratio, are appropriate.

A von Bertalanffy growth equation was fitted to the lengths-at-age of female and male fish with the traditional assumptions that the lengths-at-age are normally distributed around the values predicted from the growth equation and that the variance of this distribution is constant for each sex over all ages. However, visual examination of the residuals for each curve suggested that it was not appropriate to make the latter assumption. Further study showed that the variance of the residuals is approximately proportional to the age of the fish, as above in assumption 3 of Kimura (1980). Thus, the von Bertalanffy growth equation was fitted to the length-at-age data for each sex by using the assumption that the residuals were normally distributed, where the variance of this distribution was proportional to age but dependent on sex. That is,

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

$$\text{and } L_j = \hat{L}_j + \varepsilon_j,$$

where, for each sex, L_j = the observed length at age;
 \hat{L}_j = the estimated length-at-age;
 t_j = the age; and
 ε_j = the error associated with the j th fish.

For the growth curves for females and males, L_∞ is the mean asymptotic length predicted by the equation, k is the growth coefficient, and t_0 is the hypothetical age at which fish would have zero length if growth had followed that predicted by the equation. The errors are assumed to be normally distributed, such that $\varepsilon_j \sim N(0, c_s t_j)$, where c_s is the constant of proportionality between the variance of the residuals and age for fish of sex s . The growth equations were fitted to the observed length-at-age data for both sexes by maximizing the log-likelihood of the data. The log-likelihood for the combination of male and female fish, λ , may be written as

$$\lambda = \lambda_M + \lambda_F,$$

where λ_s = the log-likelihood associated with females or males and may be calculated as

$$\lambda_s = -\frac{n_s}{2} \log(2\pi) - \frac{1}{2} \sum_{j=1}^{n_s} \log(c_s t_j) - \frac{1}{2c_s} \sum_{j=1}^{n_s} \left\{ \frac{(L_j - \hat{L}_j)^2}{t_j} \right\},$$

and n_s = the number of fish of that sex in the length-at-age data.

The maximum likelihood estimate of c_s for each sex is given by

$$c_s = \frac{1}{n_s} \sum_{j=1}^{n_s} \left\{ \frac{(L_j - \hat{L}_j)^2}{t_j} \right\}.$$

The SOLVER routine in Microsoft EXCEL (Microsoft Corp., 2000) was used to estimate the parameters that

would maximize the log-likelihood function, by fitting the equations to the combined set of length-at-age data for both females and males.

The growth curves for the fish of each sex were compared following the likelihood ratio method described by Kimura (1980) and Cerrato (1990). The test of the likelihood ratio, Λ , that was applied was to reject the null hypothesis Ω (that there was no difference between the curves) at the α level of significance when

$$\Lambda^{-2/n} > \left(1 + \frac{q}{f_M + f_F} F_{q_{f_M + f_F}}^a \right),$$

$$\text{where } \Lambda = \left(\frac{\hat{\sigma}_{M\omega}^2}{\hat{\sigma}_{M\Omega}^2} \right)^{-n_M/2} \left(\frac{\hat{\sigma}_{F\omega}^2}{\hat{\sigma}_{F\Omega}^2} \right)^{-n_F/2}$$

and where $n = n_M + n_F$

$f = n - 3$; and

$q =$ the number of linear constraints of the form

$\theta_M = \theta_F$, where θ is one of the parameters

L_∞, k, t_0 .

M and $F =$ males and females, respectively.

This test was developed by Gallant (1975), as described by Cerrato (1990).

The growth curves were fitted under all possible parameter sets, and the best of both the 4- and 5-parameter models, i.e. those that maximized the log-likelihood, were selected. The resulting 3-, 4- and 5-parameter models were compared with the 6-parameter model by using the above test to determine which of these three models, w , was of minimum complexity and not significantly different from the 6-parameter model Ω . The model selected on the basis of these tests was the simplest model that, in the statistical sense, provided the best description of the data.

Reproductive biology

The gonads of each fish that could be sexed macroscopically were removed and weighed to the nearest 0.01 g. Each gonad was allocated to a maturity stage, based on the scheme of Laevastu (1965), but which, in the case of females, also took into account the histological characteristics of the ovaries (see "Results" section).

The percentage contributions made by the different gonadal stages in sequential 50-mm length intervals were calculated for both female and male *G. hebraicum*. The lengths at which 50% of female and male *G. hebraicum* reach sexual maturity (L_{50}) were determined by fitting the logistic curve to the percentage of female and male fish which, during the spawning period, possessed gonads at stages III to VIII (see "Results" section for rationale for using these six stages for this purpose). The logistic curve was fitted by employing a nonlinear technique (Saila et al., 1988) and by using a routine statistical method provided in SPSS (SPSS Inc., 1988). The logistic equation is $P_L = 1/(1 + e^{(a-bL)})$, where P_L is the proportion of fish with mature gonads at the mid-point of the length class, L , and a and b are constants. The L_{50} for each sex was derived

from the equation $L_{50} = \frac{-a}{b}$. The ages at which 50% of females and males reached maturity, i.e. the A_{50} , were estimated, as follows, from the inverse von Bertalanffy growth equations for the two sexes (see Stergiou, 1999):

$$A_{50} = t_0 - \left(\frac{1}{k} \right) \log \left(1 - \frac{L_{50}}{L_\infty} \right).$$

Gonadosomatic indices (GSIs) of females and males $\geq L_{50}$ at first maturity were determined from the equation

$$W1/W2 \times 100,$$

where $W1 =$ wet weight of the gonad; and

$W2 =$ wet weight of the whole fish.

Mortality

Preliminary analysis of catch curves demonstrated that the mortality estimates derived for commercially and recreationally caught fish that were greater than the MLL of 500 mm and eight years old and thus fully recruited (see "Results" section) were similar. Thus, the data from the commercial and recreational samples were pooled for estimating mortality. An estimate of the instantaneous coefficient of natural mortality, M , was determined from the von Bertalanffy growth coefficient, k , with the regression equation developed by Ralston (1987), i.e. $M = 0.0189 + 2.06k$. The instantaneous coefficient of total mortality, Z , was determined by maximizing the likelihood, when fitting the estimated age composition resulting from that mortality to the observed age composition data for those dhufish that were greater than the MLL of 500 mm and eight years old. In order to assess whether the observed age composition data reflected decreasing levels of total mortality in earlier years, the catch curve analysis was repeated with different initial ages, ranging from 10 to 30 years. Values of Z were also estimated by using the observed maximum age (t_{max}) for the sampled dhufish, employing both the regression equation reported for fish by Hoenig (1983), i.e.

$$\log(Z) = 1.46 - 1.01 \log(t_{max}),$$

and the equation for the expected value of the maximum age in a sample of size n , i.e.

$$E(t_{max}) = \frac{1}{Z} \sum_{i=1}^n \frac{1}{i} + t_c,$$

where $t_c =$ the age at which fish become fully recruited to the fishery (Johnson and Kotz, 1970, p. 216, as reported by Hoenig, 1983).

Results

Habitats of *Glaucosoma hebraicum*

Glaucosoma hebraicum <150 mm TL and <14 months old were caught regularly by trawlers offshore in water

depths of 27 to 33 m. The depth sounder indicated that these small *G. hebraicum* were most consistently caught over hard substrate that lay adjacent to reefs—a conclusion later confirmed by video footage. Although a considerable amount of effort and a variety of techniques were employed in attempts to catch fish with lengths of 150–300 mm, only a small number of fish of this size were collected. However, a few *G. hebraicum* of this length class were caught by an experienced spearfisher while diving over low-lying reefs with rock ledges <30 cm high. Large numbers of dhufish >300 mm in length were obtained from rod and hand-line fishermen who were fishing in waters that were shown by video camera and commercial echo sounders to be located over limestone and coral reef formations and, in particular, where the “drop-offs” (reef edges) were two or more metres in height.

Comparisons between number of opaque zones visible in whole and sectioned otoliths

The number of opaque zones observed in each sectioned otolith, in which up to six such zones could be seen, was the same as those visible on the same otolith prior to sectioning (Fig. 1). However, this frequently did not apply when a greater number of opaque zones were present. Furthermore, where such discrepancies occurred, the differences between the number of opaque zones detected prior to and after sectioning rose as the number of opaque zones increased. In all cases where there were discrepancies, the number of opaque zones detected after sectioning was greater than prior to sectioning. Underestimates of the number of growth zones with whole otoliths, based on comparisons with those detected in sectioned otoliths, rose from one in whole otoliths with seven to nine opaque zones to between one and seven in those with 10–21 opaque zones (Fig. 1). In otoliths with a large number of opaque zones, the differences sometimes exceeded eight and for one such otolith was as high as twelve. These comparisons demonstrated that, for validation that opaque zones are formed annually and that these zones can thus be used for aging *G. hebraicum*, experiments should be conducted on sectioned otoliths.

Validation that opaque zones are formed annually

The mean monthly marginal increments on sectioned otoliths with 2 to 16 or more opaque zones rose from a low level in January to a maximum in September, before declining precipitously to a minimum in October and then rising slightly in December (Fig. 2). They thus reached high levels in early spring, before declining markedly in mid-spring, as the outermost opaque zone became delin-

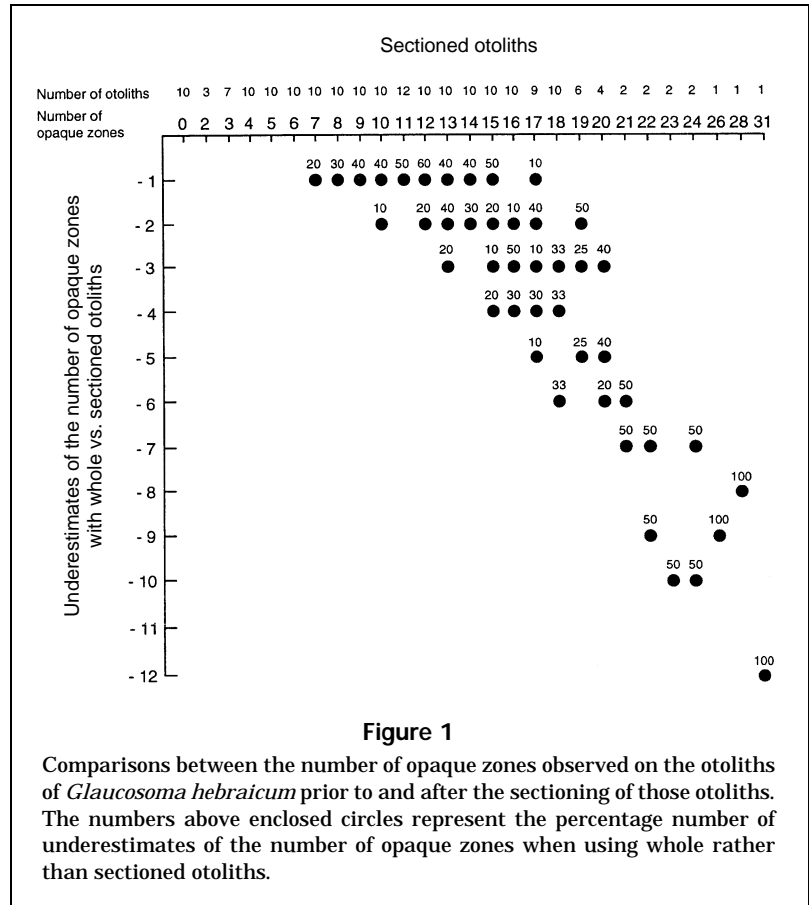


Figure 1

Comparisons between the number of opaque zones observed on the otoliths of *Glaucosoma hebraicum* prior to and after the sectioning of those otoliths. The numbers above enclosed circles represent the percentage number of underestimates of the number of opaque zones when using whole rather than sectioned otoliths.

eated through the formation of a new translucent zone, and then increased progressively in the ensuing months as the translucent region increased in width. Although fish possessing otoliths with one opaque zone were not caught in all months, the trends exhibited by the mean monthly marginal increments for those months when such fish were caught were consistent with those exhibited by otoliths with a larger number of opaque zones.

Because the mean monthly marginal increment rose and declined only once during the year, irrespective of the number of opaque zones in the otolith, a single opaque zone is laid down in the otoliths of *G. hebraicum* each year. The number of opaque zones in sectioned otoliths can thus be used, in conjunction with the birth date of *G. hebraicum* and the month when the opaque zone(s) become delineated, to age this species.

Growth of *Glaucosoma hebraicum*

Because the trends exhibited by the GSIs and stages in gonadal maturation and oocyte development demonstrated that the spawning of *G. hebraicum* peaked from late January through early February, this species was assigned a birth date of 1 February. Age 0+ *G. hebraicum* were first caught by trawling over hard substrate in April and May, when their lengths ranged from 57 to 81 mm (Fig. 3). However, substantial numbers of the 0+ age class were not

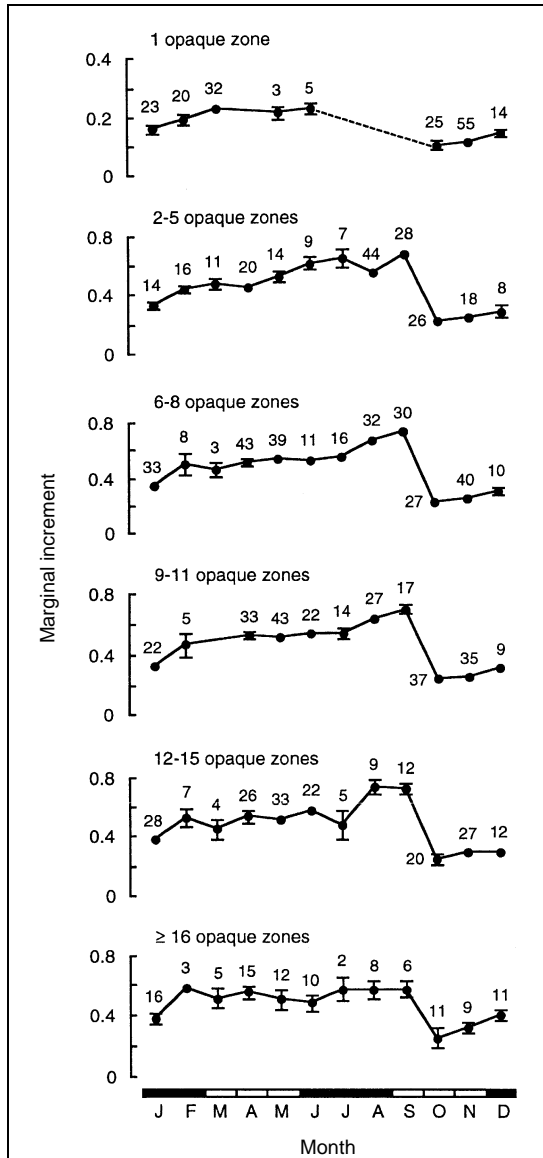


Figure 2

Mean monthly marginal increments ±1SE for sagittal otoliths of *Glaucosoma hebraicum*. Sample size is given for each month. In this Figure and Figure 5, the closed rectangles on the horizontal axis refer to summer and winter months and the open rectangles to autumn and spring months.

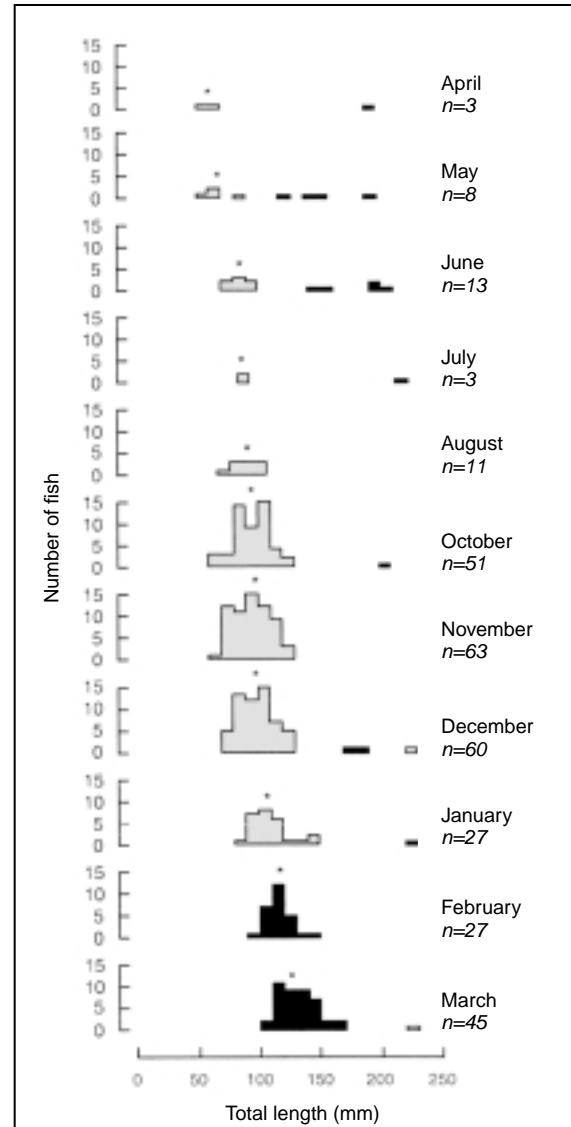


Figure 3

Length-frequency distributions for *Glaucosoma hebraicum* caught by trawling along the lower west coast of Australia by using data for corresponding months in the period May 1996 to June 1999. *denotes mean lengths of 0+ and early 1+ fish. Histograms in gray refer to 0+ fish, and those in black and white refer to 1+ and 2+ fish, respectively.

caught until October, presumably reflecting the time typically required for the 0+ age class to be recruited into these areas from those in which spawning occurs. The mean length of the 0+ age class had reached 95 mm by October, in which month the first opaque zone became delineated on the otoliths, and 108 mm by January, when fish were approaching the end of their first year of life. The mean length of the corresponding cohort, now early 1+, was 127 mm in March, after which month the number of 1+ fish caught in trawl samples declined markedly (Fig. 3).

The best of the 4- and 5-parameter growth curves were selected as the models with the largest log-likelihood at that level of model complexity. The best 4-parameter model was the curve that assumed different asymptotic lengths for the sexes, and the best 5-parameter model was that which assumed that the growth coefficients were equal.

Comparisons between the curves demonstrated that the model that assumed common growth coefficients for females and males was not significantly different ($P > 0.05$) from the more complex model, which assumed that all

parameters of the growth curves differed between the sexes. For this curve, the parameters L_{∞} , k , and t_0 and their 95% confidence limits were estimated to be 929 (908 to 949) mm, 0.111 (0.107 to 0.116)/year, and -0.141 (-0.183 to -0.100) years, respectively, for females, and to be 1025 (1003 to 1048) mm, 0.111 (0.107 to 0.116)/year, and -0.052 (-0.088 to -0.016) years, respectively, for males. The growth curves for females and males were significantly different ($P < 0.001$), with the asymptotic lengths having the most influence on the difference between the sexes. The estimated constant of proportionality between the variance of the residuals and age were 363 for females and 320 for males.

The von Bertalanffy growth curves demonstrated that females grow slightly slower than males. Thus, at ages 2 to 5, females had reached lengths of 196, 273, 342, and 404 mm, compared with 209, 294, 371, and 440 mm for males. By the time *G. hebraicum* had attained 10, 15, and 20 years, the females had reached ca. 628, 756, and 830 mm, respectively, and the males had reached ca. 689, 832, and 914 mm, respectively (Fig. 4). The maximum ages recorded for females and males were 39 and 41 years, respectively, and the maximum total lengths of females and males were 981 mm (=ca. 15.3 kg) and 1120 mm (=ca. 23.2 kg), respectively. The ages at which female and male *G. hebraicum* reach the minimum legal length for capture (500 mm TL) were 7.0 and 6.0 years, respectively.

Trends exhibited by reproductive variables

The macroscopic characteristics of the different stages in gonadal development, and of the cytological characteristics of the ovaries at different stages based on an examination of histological sections, are given in Table I.

Because stages I (virgin) and II (immature) in the development of both the ovaries and testes of *G. hebraicum* were difficult to separate macroscopically, data for these two stages were pooled in the case of both sexes. Furthermore, it is also important to recognize that spawning stage (VI) ovaries are distinguished from prespawning stage (V) ovaries almost exclusively on the basis of their possession of hydrated oocytes or postovulatory follicles (or both) when histological sections were employed to examine the ovary at a finer scale. However, because *G. hebraicum* is a multiple spawner, i.e. produces eggs in batches at intervals, any "prespawning" stage ovary may already have produced some hydrated oocytes, but been at an intermediate phase in which the next batch of yolk granule oocytes had not yet become hydrated. The prevalence of females with prespawning ovaries that had already spawned on one or more occasions would be expected to increase during the spawning period. Likewise, the main difference between prespawning and spawning testes, i.e. the ability of the testes to produce milt when subjected to physical pressure, may often represent different phases in the cyclical changes undergone in the testis during the spawning period. For the above reasons, the data on stage-V and stage-VI ovaries and testes were pooled for describing the change in compositions of the gonadal maturity stages of each sex during the year.

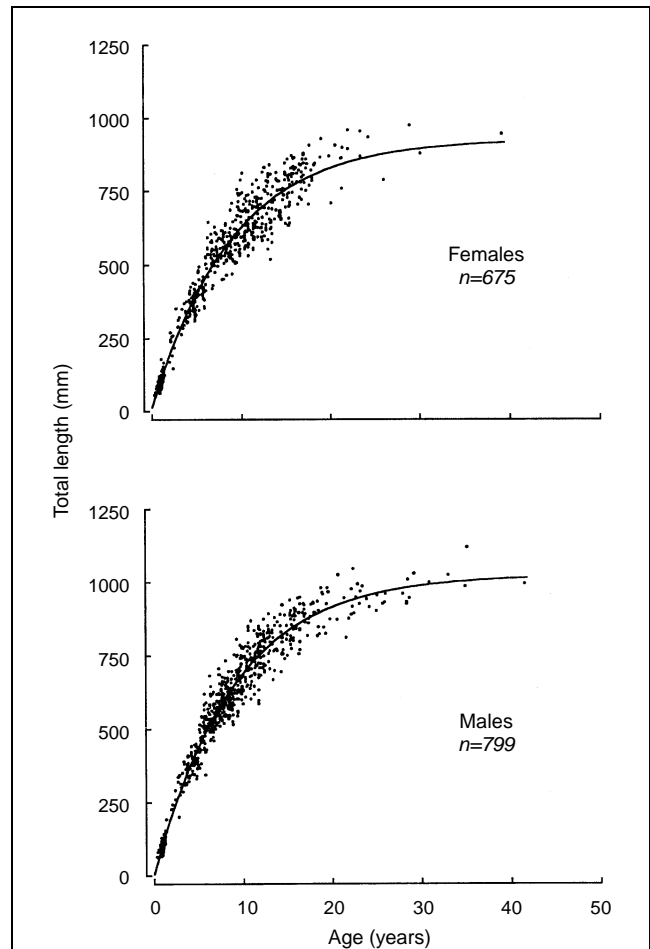


Figure 4

Von Bertalanffy growth curves fitted to length-at-age data for females and males of *Glaucosoma hebraicum* caught on the lower west coast of Australia. n = number of fish used to construct growth curves.

Between May 1996 and April 1998, the mean monthly GSIs for females of *G. hebraicum* that were greater than the L_{50} of 301 mm at first maturity were always low in winter (June to August) and early spring (September), i.e. < 1.0 but then rose sharply to reach a peak of ca. 2.8 in mid-summer (January), before declining markedly during early to mid-autumn (March and April) (Fig. 5). The trends displayed by the mean monthly GSIs for males of *G. hebraicum*, that were greater than the L_{50} of 320 mm at first maturity, paralleled those just described for females.

Because the trends exhibited by the mean monthly GSIs for females and males were the same during both 12 month periods, the percentage contributions of the different gonadal stages of the females and males of *G. hebraicum*, that were longer than the L_{50} , were pooled for each of the corresponding calendar months. The gonads of female *G. hebraicum* in July were at stages I–II, i.e. virgin or immature (Fig. 6). Fish with ovaries at stage III (developing) were first found in August, albeit only a few fish, and those at stage IV

Table 1

Characteristics of the macroscopic stages in the development of the gonads of *Glaucosoma hebraicum* and, in the case of the ovaries, the histological characteristics of each corresponding ovarian stage. Terminology for oocyte stages follows Khoo (1979).

Stage	Macroscopic appearance	Histological characteristics
I–II (virgin and immature)	Gonads very small. Ovaries transparent and oocytes not visible. Testes strandlike and gray-white.	Ovigerous lamellae highly organized. Oogonia and chromatin nucleolar oocytes and, in more advanced ovaries, early perinucleolar oocytes are present. These oocyte stages are present in all subsequent ovarian stages.
III (developing)	Gonads slightly larger than at stage I or II. Ovaries pinkish, blood capillaries visible in ovary walls. Testes white and more lobular.	Early and late perinucleolar oocytes and yolk vesicle oocytes present.
IV (maturing)	Gonads markedly larger. Ovaries reddish-orange, capillaries more conspicuous and some yolk granule oocytes visible through ovary wall. Milt is not extruded when pressure is applied to testes.	Yolk vesicle and yolk granule oocytes abundant.
V (prespawning)	Ovaries orange and occupy most of space in body cavity. Extensive capillaries in ovary walls. Milt appears when testes placed under firm pressure.	Yolk granule oocytes abundant and in tight groups.
VI (spawning)	Same as for stage V, but with hydrated oocytes visible through ovarian wall and only slight pressure required to release milt from testes.	Hydrated oocytes or postovulatory follicles (or both) present.
VII (spent)	Gonads smaller than at stages V or VI. Ovaries flaccid. Some yolk granule oocytes still visible through ovary wall. Testes pinkish-red.	Remnant yolk granule oocytes present, typically undergoing atresia.
VIII (recovering spent)	Gonads greatly reduced in size and dark red. Testes strandlike.	Lamellae not organized as in early stages of development and contain extensive scar tissue. Any remaining yolk granule oocytes are atretic.

(maturing) and stages V and VI (prespawning and spawning) were first recorded in September and October, respectively. Stage-V and stage-VI ovaries collectively became the most prevalent group in females in November and formed the most dominant group by far in December to March. The samples in February and March contained a few female fish with stage I–II ovaries, but none with ovaries at either stage III or IV (Fig. 6). These trends provide overwhelming circumstantial evidence that any female whose ovaries have developed to at least stage III by November will progress through to maturity during the following months of the spawning period. Thus, the L_{50} for females at first maturity was calculated by using the percentage of ovaries with stages III and IV, as well as those with stages V–VIII. Although females with stage-VII (spent) and stage-VIII (recovering spent) ovaries were found between January and May, the majority of ovaries were at stages I–II in the latter month and all were at stages I–II in June. The trends exhibited by the pattern of gonadal development in males were essentially the same as those just described for females and thus the L_{50} of males was likewise calculated with the percentage of testes at stages III–VIII (Fig. 7).

The following account of the trends exhibited by the oocyte composition of ovaries is based on an histological examination of the ovaries of large fish well above the L_{50} at first maturity. The oocytes in ovaries in July and August were almost exclusively at the chromatin nucleolar stage. Ovaries with yolk vesicles first appeared in September, and those with yolk granules were first found in October. Yolk granule oocytes became increasingly prevalent in ovaries in November and dominated the complement of their larger oocytes between December and March. Some of the residual yolk granule oocytes in April and all of those in May were undergoing atresia. No yolk vesicle or yolk granule oocytes were found in June. Hydrated oocytes were first found in ovaries in November and were present in many ovaries between December and March and in a few ovaries in April, but were found neither in May nor in the immediately ensuing months. Small numbers of post-ovulatory follicles were present in about a third of the ovaries of large females caught between December and March. The oocyte diameters of individual large *G. hebraicum* caught in each month of the spawning period produced a series of modes (data not shown).

Length and age at maturity

The sex of *Glaucosoma hebraicum* was not able to be determined by macroscopic examination of the gonads until it had reached ca. 150 mm in length. During the main part of the spawning period, i.e. December to March, the gonads of all female and male *G. hebraicum* <250 mm were at the earliest stages of development, i.e. I-II (Fig. 7). Gonads at stages III-VIII were first found in the 250-299 mm length class of females and in the 300-349 mm length class of males. The presence of such gonads demonstrated that the fish were maturing or that spawning was occurring or had been completed (see earlier). The prevalence of ovaries at stages III-VIII increased to ca. 80% in the 300-349 mm length class and to 100% in all females >450 mm. The gonads of all males >450 mm were at stages III-VIII (Fig. 7). The L_{50} 's for the lengths of female and male *G. hebraicum* at first maturity, derived from the logistic curve

fitted to the percentage contributions of fish with gonads at stages III-VIII in sequential 50-mm length classes, were 301 and 320 mm, respectively (Fig. 7).

Individual *G. hebraicum* could first be sexed macroscopically during their second year of life. Although relatively few two-, three- and four-year-old fish were caught, the trends exhibited by the proportion of gonads at stages III-VIII in both sexes during the spawning period were consistent. One female and no males at two years of age possessed gonads at stage III or greater (Fig. 8). However, 50% of three-year-old female and male fish, and all five-year-old females and all six-year-old males possessed such gonads and were thus regarded as mature. The A_{50} 's for the age at first maturity of females and males were 3.4 and 3.3 years, respectively.

Mortality

Using the regression equation developed by Ralston (1987), in combination with the estimated value for the von Bertalanffy growth coefficient, $k = 0.111/\text{year}$, we estimated the instantaneous coefficient of natural mortality, M , to be 0.25/year. The catch curve analysis of the combined age composition data, for the 620 dhufish older than 9 years and longer than the MLL (Fig. 9), produced an estimate of the instantaneous coefficient of total mortality, Z , of 0.21/year (95% confidence interval: 0.19 to 0.23/year). The estimate of Z remained at about this level as the initial age was increased to 15 years and then declined to ca. 0.15/year at 24 to 27 years (Fig. 9). It subsequently became less precise as the initial age increased. An estimate of Z of 0.10/year was obtained when the observed maximum age of 41 years was substituted into Hoenig's (1983) regression equation. However, when the sample size of 620 fish was taken into account, with the expression for the expected maximum age (Hoenig 1983, Appendix A), Z was estimated to be 0.22/year.

Discussion

Ontogenetic changes in habitat of *Glaucosoma hebraicum*

Extensive sampling for *G. hebraicum* during the present study, allied with data obtained with an echo sounder and video footage, demonstrate that this species changes habitat as it increases in size. Thus, *G. hebraicum* <150 mm was found to live in areas near reefs where the substrate is firm and sponges often occur (Bergquist and Skinner, 1982). The reduction in the numbers of 1+ dhufish caught by trawling in this type of habitat in late autumn, when their lengths were about 130 mm, probably reflects a movement by the members of this

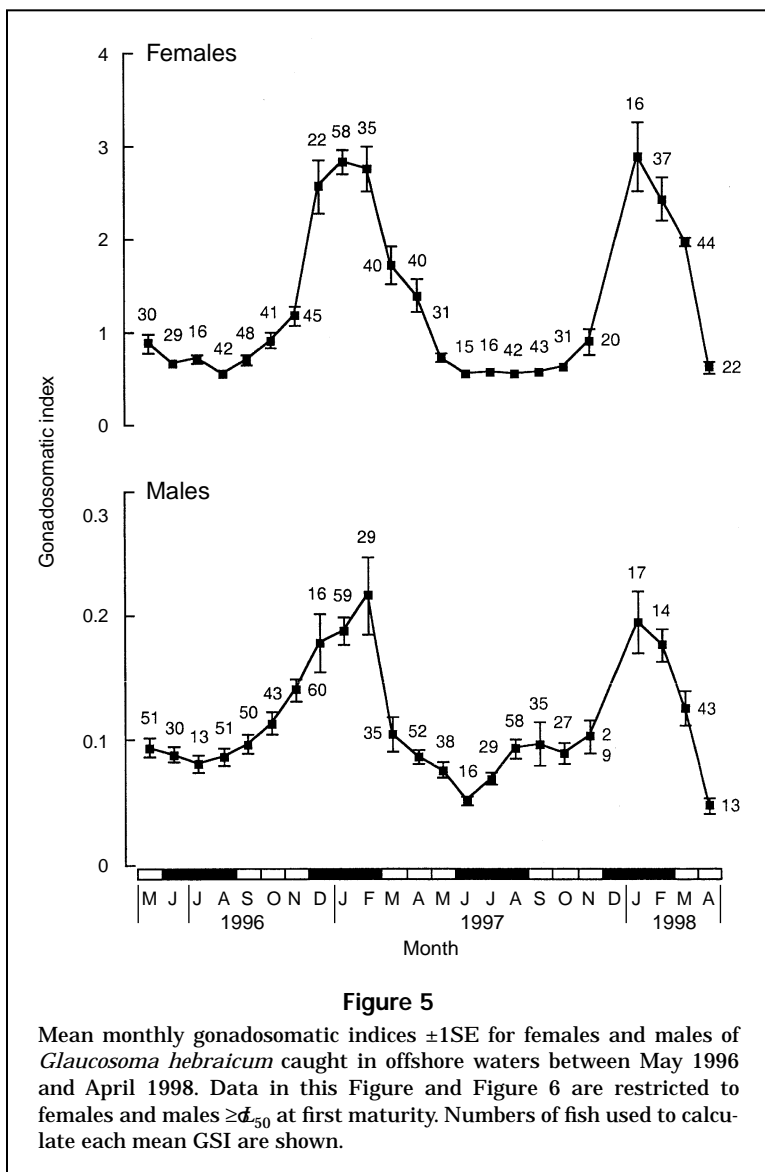


Figure 5

Mean monthly gonadosomatic indices $\pm 1\text{SE}$ for females and males of *Glaucosoma hebraicum* caught in offshore waters between May 1996 and April 1998. Data in this Figure and Figure 6 are restricted to females and males $\geq L_{50}$ at first maturity. Numbers of fish used to calculate each mean GSI are shown.

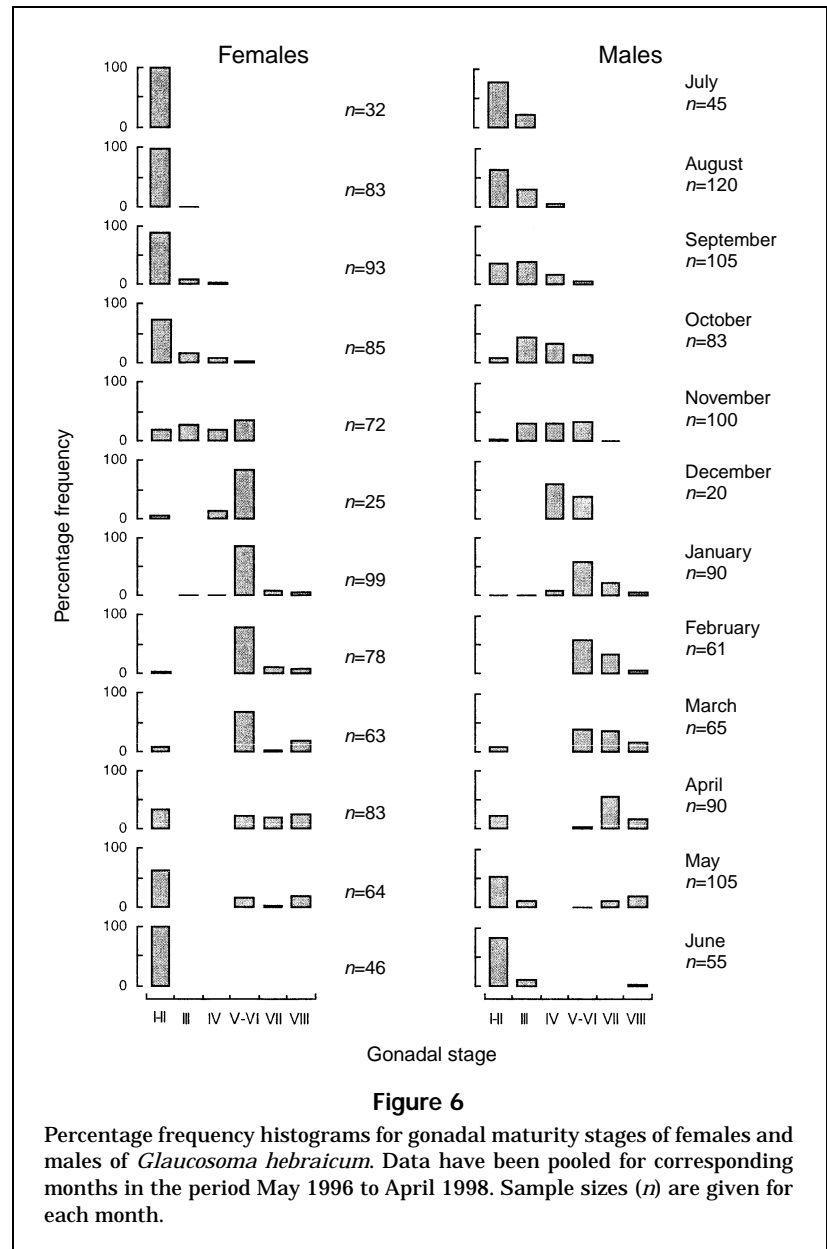
cohort, as they increase in size, from a habitat that could be trawled to one where reefs occur and where it was not possible to trawl. This conclusion is supported by the fact that the few dhufish of 150–300 mm that were caught were collected from low-lying reefs, i.e. reefs that contained rock ledges up to 30 cm in height. In contrast, *G. hebraicum* >300 mm typically occupy areas where there are substantial limestone and coral reef formations and their large size would make them less susceptible to predation in a habitat where large predatory species, such as the Samson fish (*Seriola hippos*) and the pink snapper (*Pagrus auratus*) are found (Hesp, personal obs.).

Aging

The trends exhibited by the marginal increments on sectioned otoliths of *G. hebraicum* show that an opaque zone is formed annually in the otoliths of this species. However, comparisons between the number of opaque zones on individual otoliths prior to and after sectioning demonstrate that, after this species has reached six years in age, one or more of these zones often become visible only after the otolith has been sectioned. This demonstrates that earlier estimates of the age of older *G. hebraicum*, which were based on the number of opaque zones visible in whole otoliths (Sudemeyer et al.¹), were almost certainly often too low.

An inability to detect all of the opaque zones in the whole otoliths of older fish is largely attributable to the fact that, as the otolith increases in width, it becomes increasingly difficult to distinguish between the zones at the periphery of the otolith. This problem parallels the situation recorded for several other medium-size to large teleosts, such as Pacific hake (*Merluccius productus*) (Beamish, 1979), starry flounder (*Platyichthys stellatus*) (Campana, 1984) and blue-spotted flathead (*Platycephalus speculator*) (Hyndes et al., 1992). Our results demonstrate that, although most *G. hebraicum* are less than 25 years old, some females and males live for longer than 30 years and very occasionally for up to about 40 years.

Other species that are typically caught by commercial and recreational rod and hand-line fishermen when fishing for dhufish include pink snapper (*Pagrus auratus*), Sampson fish (*Seriola hippos*), silver trevally (*Pseudocaranx dentex*), breaksea cod (*Epinephelides armatus*), and occasionally also King George whiting (*Sillaginodes punctata*). The maximum total lengths and weights recorded for these five species are 1300 mm and 19.5 kg for pink



snapper, 1753 mm and 53.6 kg for Samson fish, 938 mm and 10.0 kg for silver trevally, 550 mm and 2.9 kg for breaksea cod, and 690 mm and 4.8 kg for King George whiting, compared with 1219 mm and 25.8 kg for dhufish (Hutchins and Thompson 1995).

Although reliable data have been obtained for the age and growth of a number of commercial and recreational fish species that live in nearshore coastal or estuarine waters in southwestern Australia (e.g. Chubb et al., 1981; Hyndes et al., 1992, 1996; Hyndes and Potter, 1996, 1997; Laurenson et al., 1994; Fairclough et al., 2000; Sarre and Potter, 2000), comparable data for those species that are found in and around reefs in deeper waters in southwestern Australia are restricted to those recorded for *G. hebraicum* in this paper and for the King George whiting *Sillaginodes*

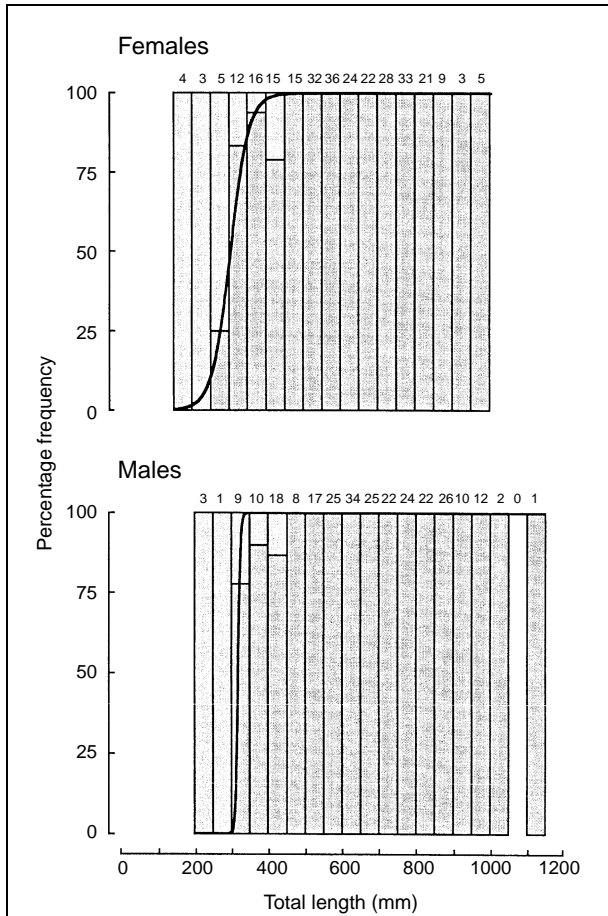


Figure 7

Percentage frequency of occurrence of gonads at stages I-II (□) and stages III-VIII (■) in each sequential 50-mm class of female and male *Glaucosoma hebraicum* caught between December and March. The logistic curve has been fitted to the data for fish with gonads at stages III-VIII. The sample size is given for each length class.

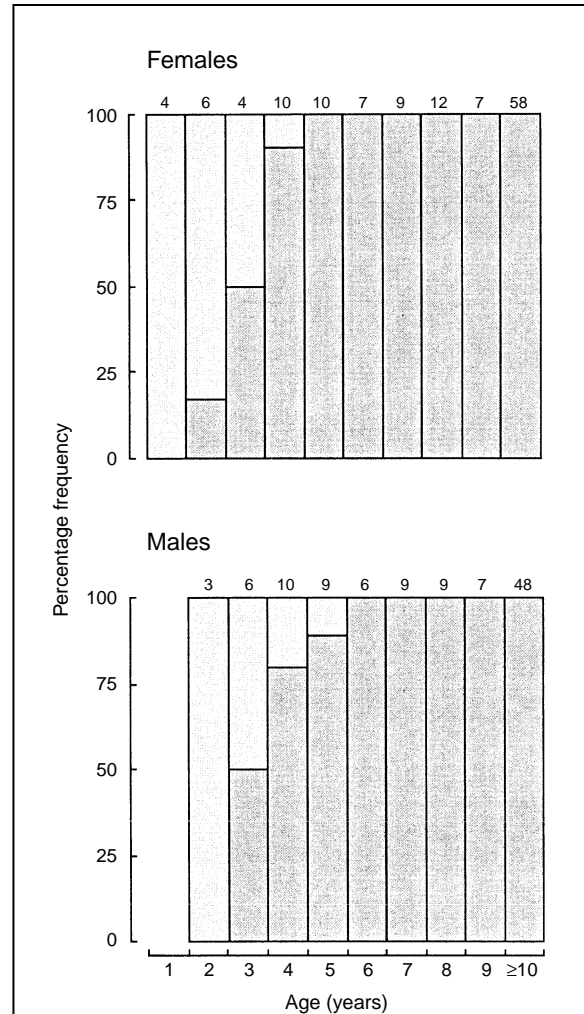


Figure 8

Percentage frequency of occurrence of gonads at stages I-II (□) and stages III-VIII (■) in each sequential age class of female and male *Glaucosoma hebraicum* caught between December and March. The sample size is given for each age class.

punctata by Hyndes et al. (1998). Using data from the lower west coast of Australia, Hyndes et al. (1998) estimated the von Bertalanffy growth parameters, L_{∞} , k , and t_0 , for King George whiting to be 538 mm TL, 0.47/year, and 0.13 years, respectively, for females, and 500 mm TL, 0.53/year and 0.16 years, respectively, for males. Although there are no published studies on the growth of pink snapper and silver trevally in Western Australia, the growth of these two species has been investigated in New Zealand by Francis et al. (1992) and by James (1984) respectively. The parameters L_{∞} , k , and t_0 were estimated to be 720 mm FL (fork length), 0.106/year and -0.75 years, respectively, for pink snapper, and ranged from 436 to 448 mm FL, from 0.27 to 0.43/year and from -1.6 to -0.6 years, respectively, for silver trevally. Although the growth coefficient, k , for dhufish, i.e. 0.111/year, was similar to that for pink snapper, it was appreciably less than that for both King George whiting and

silver trevally. Dhufish had an asymptotic length ca. 35% greater than that of pink snapper and approximately twice those of King George whiting and silver trevally.

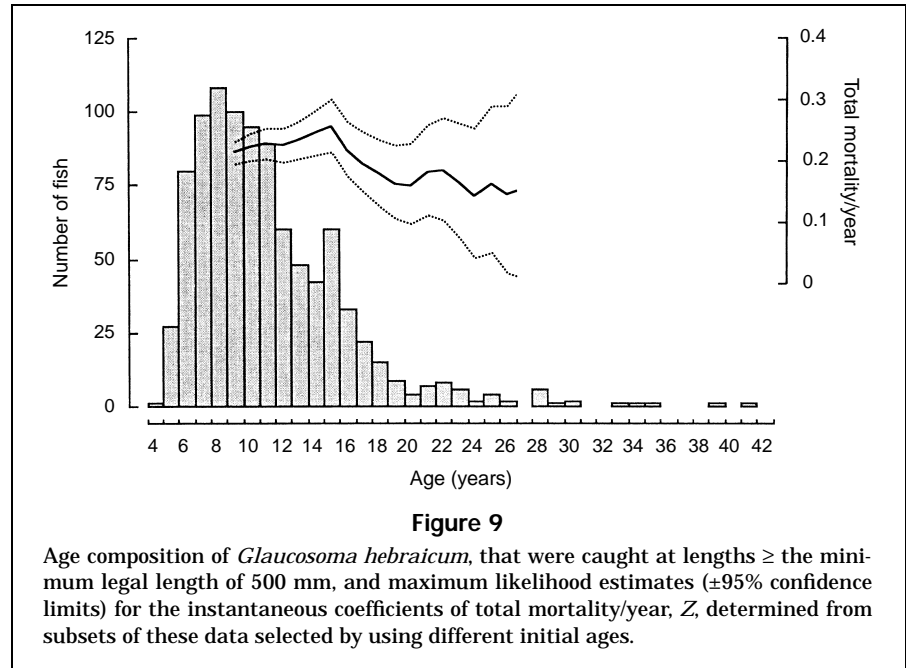
The lengths of females at maturity have been reported as ca. 350 mm FL for silver trevally (James, 1984) and 413 mm TL for King George whiting (Hyndes et al., 1998) and have been estimated as 237 mm FL for pink snapper (calculated from Crossland, 1977). Although maturity is first achieved by the females of snapper and dhufish at 30% of their respective asymptotic lengths, it is attained by the females of King George whiting and silver trevally at 75–80% of their asymptotic lengths. This finding implies that the last two species have a higher reproductive load *sensu* Cushing (1981). Thus, although these four species reach maturity and begin to occupy promi-

ment reefs at similar lengths, the growth of silver trevally and King George whiting slows after maturation, whereas that of snapper and dhufish continues appreciably after they have reached maturity.

Spawning location, period, and mode

Glaucosoma hebraicum with gonads at stages VI (spawning) and VII (spent) were caught in waters ranging from 10 to 150 m in depth and at distances of 3 to 50 km from the shore and between latitudes 28°55' and 32°45'S. Thus, the spawning of dhufish is not apparently restricted to any particular water depth or region along the coast. However, because *G. hebraicum* greater than 300–320 mm in length (their size at first maturity) were almost invariably caught only around limestone or coral reef formations, this species apparently spawns in the vicinity of reefs.

Because hydrated eggs and postovulatory follicles were found in at least some of the ovaries of large females in each month between November and April, it is evident that *G. hebraicum* spawn between the end of spring and middle of autumn. Although some fish commenced spawning in November, the mean GSI of female fish in that month was still well below its maximum. This indication that only a small amount of spawning occurs in November is consistent with the fact that many of the ovaries of large fish were still at stages III and IV. Although most of the ovaries of large females caught in May 1997 contained some vitellogenic oocytes, these oocytes were usually undergoing atresia and the ovaries of other large fish in that month were either spent or resting. Furthermore, none of the ovaries of large *G. hebraicum* caught in May contained hydrated oocytes. This finding provides strong evidence that the spawning period does not extend into May. There is also strong evidence that spawning peaks in January and February. For example, by January, the ovaries and testes of most large fish were at stages V or VI, i.e. prespawning or spawning, and, for the first time, some were spent or even recovering spent (stages VII and VIII). The maintenance of the GSIs of females at their maxima in both January and February is attributable to the fact that, because *G. hebraicum* is a multiple spawner, new batches of hydrated oocytes were continually being developed in the ovary during these two months. However, the GSIs of females and males both declined precipitously in March, which demonstrates that, in the case of ovaries, the release of eggs during spawning was not being compensated for by a comparable production of new batches of mature eggs. As spawning activity peaked in January and February, it was appropriate to use 1 February as the birth date of *G. hebraicum* when assigning an age to each fish.



The fact that, during the spawning season, mature ovaries of *G. hebraicum* often contained yolk vesicle, yolk granule, and hydrated oocytes and, in some cases, also postovulatory follicles, implies that this species is a multiple spawner *sensu* deVlaming (1983), i.e. individual females release eggs on more than one occasion in a spawning season. The oocytes of individual female *G. hebraicum* during the spawning period ranged widely in size and, in many cases, their diameters formed relatively discrete modes in oocyte diameter-frequency distributions. The ovaries of *G. hebraicum* thus contain batches of oocytes that are presumably released at different times. Multiple-batch spawning over a protracted period enables a greater total number of eggs to be produced and released during a spawning period and results in eggs becoming discharged at different times (McEvoy and McEvoy, 1992), which would increase the overall chance of recruitment success.

Implications of the biology of *Glaucosoma hebraicum* for fisheries management

The age composition data for dhufish older than 9 years and larger than the MLL reflect an average level of the instantaneous coefficient of total mortality, Z , of 0.21/year. This value is consistent with the estimate obtained from the observed maximum age, taking into account the sample size of 620 fish (Hoenig, 1983). The much lower value obtained for Z , with Hoenig's (1983) regression equation for fish, i.e. 0.10/year, does not take into account sample size.

The estimate of the instantaneous coefficient of natural mortality, M , of 0.25/year, that was calculated with Ralston's (1987) equation, exceeds the average value of 0.21/year for the instantaneous coefficient of total mortality, which was estimated from the catch curve. Examination of the residuals from the regression line fitted by Ralston (Fig. 8.1 in

Ralston, 1987) suggests that the precision of this estimate of the instantaneous coefficient of natural mortality is likely to be relatively low. It was therefore concluded that the value for M derived from Ralston's equation represented an overestimate. A more detailed examination of the catch curve data suggested, but was unable to demonstrate conclusively, that the level of total mortality experienced by the older fish when they were young was less than that which is now being experienced by the population. Indeed, if the decline in the estimated value for Z , displayed in Fig. 9, was extrapolated to an age of 40 years, the total mortality exhibited by the oldest age classes (when, as young fish, they first became fully vulnerable to the fishery) would be ca. 0.1/year. Such a value, which might be only slightly greater than the natural mortality, matches the estimate of Z calculated from the observed maximum age with Hoenig's (1983) regression equation. However, such agreement may be fortuitous because the latter estimate should represent the total mortality experienced by the fish within the sample, i.e. from age 9, rather than just the mortality of the older fish. Nevertheless, if the level of natural mortality, M , is ca. 0.1/year and the average level of instantaneous coefficient of total mortality, Z , from age 9 years is ca. 0.21/year, the current level of fishing mortality, F , would exceed 0.11/year.

In the nearshore waters along the lower west coast of Australia where this species is most heavily fished, the abundance of *G. hebraicum* has declined to a level that is of concern to fishermen. Numerous anecdotal reports indicate that commercial and dedicated recreational fishermen, such as those who provided the samples for this study, now tend to move further offshore in order to obtain catches of *G. hebraicum* comparable with those they used to obtain in waters closer to the coast. However, many recreational fishermen still continue to fish for *G. hebraicum* (and other species) in the traditional areas where dhufish were fished in the past. The expansion of the fishery for dhufish to include waters farther offshore, allied with the increasing use of global positioning systems (GPSs) to improve fishing efficiency, is increasing the level of exploitation of the stock as a whole.

The fact that there are indications that the fishing-induced mortality of dhufish may now exceed natural mortality and that ongoing expansion in the extent to which fishermen are moving offshore (and also, in the case of recreational fishermen, in a northwards and southwards direction from the main metropolitan region of Perth) will further increase fishing pressure, is of concern to the managers responsible for the fishery for *G. hebraicum*. However, because our sampling regime was not designed specifically at determining the levels of fishing mortality to which *G. hebraicum* is being subjected, there is clearly a need to undertake a study in which the main aim is to achieve this objective. If such research were to confirm our preliminary findings that fishing mortality is reaching an unacceptable level, there will be an urgent need to use the biological data produced during the current study to refine the management plans designed to conserve this species.

Female and male *G. hebraicum* first reach sexual maturity at the end of their third year of life when they are just

over 300 mm in length and they reach 500 mm, the MLL for capture, when they are about 7 and 6 years old, respectively. Thus, on average, the female and male dhufish that live until they reach the MLL will have had the opportunity to have spawned for four and three years, respectively, before they can legally be retained following capture. Ongoing research at the state fisheries laboratory in Western Australia has indicated that ca. 50% of fish caught in waters of 20–30 m depth die on being released back into the water and that this percentage increases to ca. 95% for fish brought to the surface from depths greater than 40 m (Moran²). Thus, the use of a MLL is likely to be of only limited value for conserving this species as fishing effort continues to increase. It is therefore important to introduce measures that will conserve *G. hebraicum* by maintaining the catches of this species at a level consistent with the requirements for ecological sustainability. Examples of such management controls might include closing areas to commercial and recreational fishing (particularly those around reefs that are especially heavily fished) introducing quotas for commercial fish catches, making adjustments to the number of commercial licenses, further restricting the bag limit for recreational fishermen, and limiting the number of recreational fishermen that can fish in a given area. Furthermore, because the Fremantle Maritime Centre has successfully cultured *G. hebraicum* (Cleary et al.³), there is also now the potential for restocking this species in areas in which it has become severely depleted.

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