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Age, growth, mortality and population characteristics of the pearl perch, *Glaucosoma buergeri* Richardson 1845, from deeper continental shelf waters off the Pilbara coast of north-western Australia

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Summary

Pearl perch, *Glaucosoma buergeri* Richardson 1845, from deeper waters (> 100 m depth) on the continental shelf of north-western Australia were aged by examining transverse sections of their sagittal otoliths. Ages were assigned based on counts of alternating opaque and translucent zones (annuli). Otolith length and breadth (width) increased linearly with fish length, whereas otolith weight increased linearly with fish age. The continuous growth of the otoliths provides some evidence that the opaque and translucent zones used to estimate age in this study are formed on a regular basis. Parameters of the length–weight relationship were estimated, along with parameters of the von Bertalanffy growth function. The generalised von Bertalanffy growth function (total length-at-age, both sexes combined) for *G. buergeri* was $L_t = 512.7\ (1 - e^{-0.139(t\ +\ 0.89)})$. There was no significant differential growth between the sexes in observed length-at-age. The oldest individual found was a male *G. buergeri* estimated to be 26 years of age. The annual instantaneous rate of natural mortality (M) was estimated to be 0.14. The slow growth, long life and low natural mortality rate indicate that *G. buergeri* is vulnerable to overfishing and that harvest strategies for this species should be conservative, given its low production potential.

Introduction

Pearl perch or northern pearl perch, *Glaucosoma buergeri* Richardson 1845 (Glaucosomatidae), are distributed along the west coast of Western Australia from Shark Bay (25°S) in the south to the Timor Sea in the far north of the State (Newman, unpublished data; McKay 1997). Worldwide, *G. buergeri* is found only from southern Japan, south along the north China coast to Taiwan and Vietnam, throughout Indonesia and north-western Australia (McKay 1997). It is found in moderate depths (80–150 m) along the continental shelf and is often associated with hard bottom and epibenthic communities. *Glaucosoma buergeri* is primarily of commercial importance to the fish trawl fisheries of Western Australia with annual landings in 1996–97 of more than 55 000 kg (Fisheries 1999). However, *G. buergeri* is only an incidental and minor component of the catch of commercial trap and line fishers of Western Australia.

Estimation of the demographic parameters of fish populations, particularly the rates of growth and mortality, are essential to assessment of the population dynamics, potential yields and management of fisheries resources. Although fish ages can be derived indirectly from length frequency data and tag-release experiments, the use of hard parts of fish are generally considered as the best method of determining the age of fish. Fish otoliths provide reliable estimates of age because they are not subject to resorption, remodelling or regeneration (Secor et al. 1995).

Alternating opaque and translucent bands (annuli) in sectioned otoliths of many species of tropical reef fishes have been shown to be formed once per year by direct (e.g. tetracycline labelling) and indirect (marginal increment analysis) age validation techniques (e.g. Ferreira and Russ 1992, 1994; Fowler and Doherty 1992; Cappo et al. 2000). Furthermore, the relationship between otolith weight and fish age is usually independent of fish size, suggesting that otolith weight can be used as an objective method of age determination (Worthington et al. 1995a, 1995b).

Studies of the age, growth and mortality rates of *G. buergeri* have not previously been undertaken off the Pilbara coast of north-western Australia or elsewhere. Knowledge of the demographic parameters of these species will assist in the development of management models for the sustainable exploitation of these fishes. The present work investigated the age, growth and mortality rate of *G. buergeri* off the Pilbara coast of north-western Australia.

Materials and methods

Samples of *G. buergeri* ($n = 256$) were obtained between July 1997 and September 1999 principally from a fish trawl research programme off the northern (Pilbara) coast of tropical Western Australia (116–120°E) at depths from 100 to 200 m. Additional samples for age and growth analysis were also collected from the commercial fish trawl fishery off the Pilbara coast at depths of 50–100 m.

All fish were measured to the nearest millimetre total length (TL), fork length (FL) and standard length (SL), and weighed to the nearest gram total weight (TW). All individuals were measured lying on the left side, with the body flattened and the jaw closed. Where possible, the sex was determined by macroscopic examination of the gonads. The sagittal otoliths were removed by opening the otic bulla from under the operculum. Otoliths were then washed in fresh water and stored in envelopes prior to processing.

Length–weight models

The relationship between length and weight was described by the power relationship:

$$W = aL^b,$$

where W is total weight (g) and L is total length or fork length (mm). The relationship between length and weight was fitted to a log-transformed set of data, and the parameters were back-transformed (with correction for bias) to the above form following the method described by Sprugel (1983). Measurements of fish length (TL, FL, SL) were used to derive length conversion equations: $\mathrm{TL} = a + b(\mathrm{FL})$; $\mathrm{TL} = a + b(\mathrm{SL})$; $\mathrm{FL} = a + b(\mathrm{TL})$; $\mathrm{FL} = a + b(\mathrm{SL})$; and $\mathrm{SL} = a + b(\mathrm{FL})$.

Analysis of covariance ($\alpha = 0.05$) was used to determine whether there were significant differences in the total weight-at-length (TL) relationships between sexes. Length and weight data were transformed to a natural logarithm function ($\log_e x$) to satisfy assumptions of normality and homogeneity. Multiple comparisons were performed using Tukey's honestly significant difference (HSD) test (Day and Quinn 1989).

Otolith preparation and age determination

The left and right sagittae were weighed (to 0.01 mg) and measured along three axes [total length, breadth and height (thickness) through the central core of the otolith] to the nearest 0.01 mm using digital callipers. These dimensions were related to the length and age of the fish using linear regression techniques.

Age determination was based on the analysis of transverse sections of otoliths. One sagitta per fish was randomly selected and embedded in epoxy resin. A thin transverse section (250–400 μm) was made through the core of the otolith from the dorsal apex to the ventral apex with a low-speed jewellery saw. Three sections were made from each otolith to assist in age estimation. These sections were then examined under a dissecting microscope at 20–50× magnification on a black background with reflected light.

Ages were assigned based on counts of annuli (alternating opaque and translucent bands) from sectioned otoliths. The precision of age estimates was assessed to determine the level of confidence that can be placed in the interpretation of otolith structure. Each otolith was examined independently on three separate occasions. For those fish whose counts differed, the final count was used for analysis of age and growth, since by this time considerably more experience had been gained in the interpretation of the structure of these otoliths. The precision of age estimates was calculated using the index average percentage error (IAPE) of Beamish and Fournier (1981). Greater precision is achieved when the IAPE is minimized.

Growth and mortality models

The observed total length-at-age of *G. buergeri* indicated asymptotic growth and the von Bertalanffy growth function (VBGF) was fitted to estimates of length-at-age using non-linear least squares estimation procedures. The VBGF is defined by the equation:

$$L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$$

where L_t = length at age t; L_∞ = asymptotic length; K = Brody growth coefficient and defines the growth rate towards L_∞; t = age of the fish; and t_0 = the hypothetical age at which a fish would have zero length if it had always grown in a manner described by the equation. Minimum, maximum and mean lengths and ages were also recorded from the Pilbara population. A modified analysis of the residual sum of squares was used to compare VBGFs between sexes (Chen et al. 1992). The hypothesis being tested is that there is a single underlying growth curve applying to both sexes.

Estimates of the instantaneous rate of total mortality (Z) were obtained using the age-based catch curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish in each age class (N_t) was plotted against their corresponding age (t) and Z estimated from the descending slope, b. Estimates of the survival rate of each species (S) were then calculated by $S = e^{-Z}$ (Ricker 1975). The use of catch curves implies relatively constant recruitment and mortality rates across time periods corresponding to the range of ages in the sample.

Samples of *G. buergeri* obtained from the 100–200 m depth zone off the Pilbara coast were representative of a relatively unfished stock as fishing activity in this zone has been limited, as they are somewhat remote from the inshore fishing grounds. The instantaneous total mortality rate estimated from the catch curve was therefore considered to provide a good estimate of the instantaneous natural mortality rate (M).

Instantaneous natural mortality rates (M) were also obtained from empirical equations such as the general regression equation of Hoenig (1983) for fish, where: $\log_e Z = 1.46–1.01 \log_e t_{\max}$ ($t_{\max}$ is the maximum age in years); and Pauly (1980) based on parameters of the VBGF and mean water temperature (in °C), where: $\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$, and the mean annual water temperature for the Pilbara coast (116–120°E) is 26.9 °C.

Estimating a limit reference point for fisheries management

Patterson (1992) reported that exploitation rates above 2/3 M have been associated with stock declines, whereas exploitation rates below this level have resulted in stock recovery. This level of fishing mortality has been adopted as a limit reference point for fishery managers (F_{limit}). A limit reference point represents a state of a fishery resource, which is considered to be undesirable and which management action should avoid (Caddy and Mahon 1995). Calculation of F_{limit} requires an estimate of the natural mortality rate, M, since $F_{\mathrm{limit}} = 2/3\ M$.

Results

Length–weight models

Length–weight relationships were calculated separately for males, females and for both sexes combined (Table 1). Analysis of covariance of weight-at-length was not significantly different between sexes for *G. buergeri* ($F = 3.14$; d.f.: 1301; $P > 0.05$). The relationship between total weight and

Table 1
Length–weight relationships of *G. buergeri* from the Pilbara coast of north-western Australia. Estimates were obtained of the parameters a and b of the relationship $W = aL^b$, the sample size (n) and the regression r^2 value (lengths used are TL or FL in mm and the weight is TW in g)

Group	a	b	n	r^2
G. buergeri (TL-all fish)	8.490×10^{-5}	2.725	355	0.998
G. buergeri (TL-male)	8.390×10^{-5}	2.729	215	0.998
G. buergeri (TL-female)	9.375×10^{-5}	2.707	191	0.998
G. buergeri (FL-all fish)	7.797×10^{-5}	2.763	356	0.998
G. buergeri (FL-male)	7.652×10^{-5}	2.768	216	0.998
G. buergeri (FL-female)	8.519×10^{-5}	2.747	191	0.998

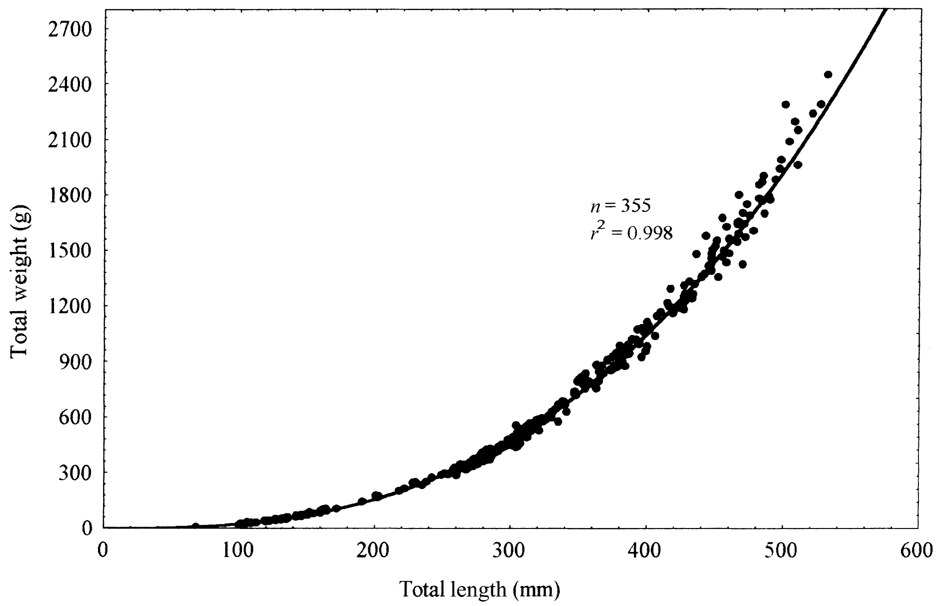

Fig. 1. Length–weight relationship for *G. buergeri* off the Pilbara coast of north-western Australia

Table 2
Length conversion relationships for *G. buergeri* from the Pilbara coast of north-western Australia. Estimates were obtained of the parameters *a* and *b* of the length–length relationships, sample size (*n*) and regression r^2 value (all lengths are in mm)

Length–length relationship	*n*	r^2
TL = −2.711 + (1.0575 × FL)	257	0.9996
TL = 5.742 + (1.3194 × SL)	257	0.9973
FL = 2.684 + (0.9452 × TL)	257	0.9996
FL = 7.997 + (1.2476 × SL)	257	0.9977
SL = −5.871 + (0.7997 × FL)	257	0.9977

total length is presented in Fig. 1. Length conversion equations were derived for TL, FL and SL (Table 2).

Otolith morphology, interpretation and otolith growth

The sagittae of *G. buergeri* are laterally compressed, elliptical structures, with a slightly concave distal surface, a slightly pointed rostrum and postrostrum and a pointed posterior projection on the dorsal surface. A curved sulcus crosses the proximal surface longitudinally. The depth of the sulcal groove increases with the increasing fish age. Annuli were usually counted in the region from the primordium to the proximal surface along the ventral side of the sagitta. Annuli in this region were usually well defined.

The precision of otolith readings of *G. buergeri* was moderately high, with the IAPE, 8.80%. The higher the level of agreement among readings, the lower the IAPE. Hence, otoliths were interpreted in a similar manner on each occasion.

Otolith length and breadth were better predictors of fish length in *G. buergeri* than otolith weight and height, although all variables accounted for more than 90% of the variability in length (Table 3). In contrast, otolith length and breadth were poor predictors of age for *G. buergeri* (Table 3). Otolith weight and height were both good predictors of fish age, accounting for 91.2 and 90.6% of the variability in age of *G. buergeri* (Table 3). The relationship of otolith weight to fish age for *G. buergeri* (Fig. 2) is considered more robust than the otolith height–fish age relationship as there is a reduced chance of incurring measurement error.

Growth and mortality models

All samples of *G. buergeri* were obtained from fish trawl catches, with the trawl net selecting against individuals less than 1 year of age and less than 90 mm FL (Figs 3, 4). Although few fish were retained in the 0+ age class, a large number of individuals were caught which were less than 200 mm and were represented in the 1+ , 2+ and 3+ year classes (Figs 3, 4).

The von Bertalanffy growth curve was fitted to lengths-at-age for all *G. buergeri* (Fig. 5), and separately for each sex

Table 3
Comparison between otolith dimensions and length and age of *G. buergeri*. The predictive equations are of the simple linear regression form $y = a + bx$. For regression analyses fish length (TL) and age were used as the dependent variables (all regressions were significant at $P < 0.001$). The standard error (SE) of the estimate is a measure of the dispersion of the observed values about the regression line

Dependent variable	Independent variable	Sample size	Equation	r^2	SE of estimate
TL	OW	253	TL = 135.5 + (316.6 × OW)	0.922	36.99
TL	OL	252	TL = −81.35 + (25.98 × OL)	0.986	15.87
TL	OB	257	TL = −190.2 + (46.30 × OB)	0.945	30.69
TL	OH	257	TL = −114.5 + (144.0 × OH)	0.907	40.16
Age	OW	252	Age = 0.123 + (13.62 × OW)	0.912	1.701
Age	OL	251	Age = −8.029 + (1.039 × OL)	0.840	2.289
Age	OB	256	Age = −11.90 + (1.807 × OB)	0.767	2.757
Age	OH	256	Age = −10.75 + (6.238 × OH)	0.906	1.753

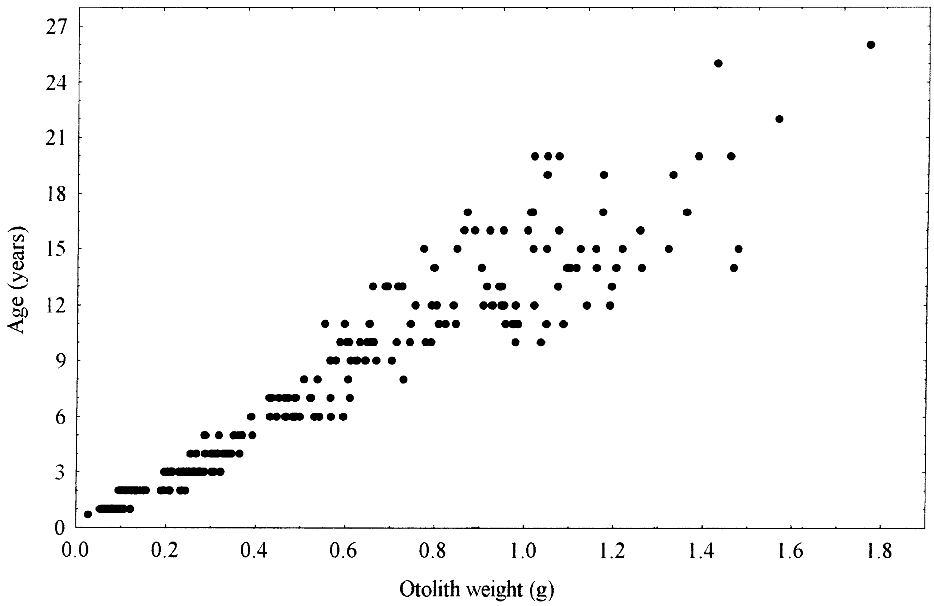

Fig. 2. Relationship of fish age to otolith weight (g) for *G. buergeri* off the Pilbara coast of north-western Australia

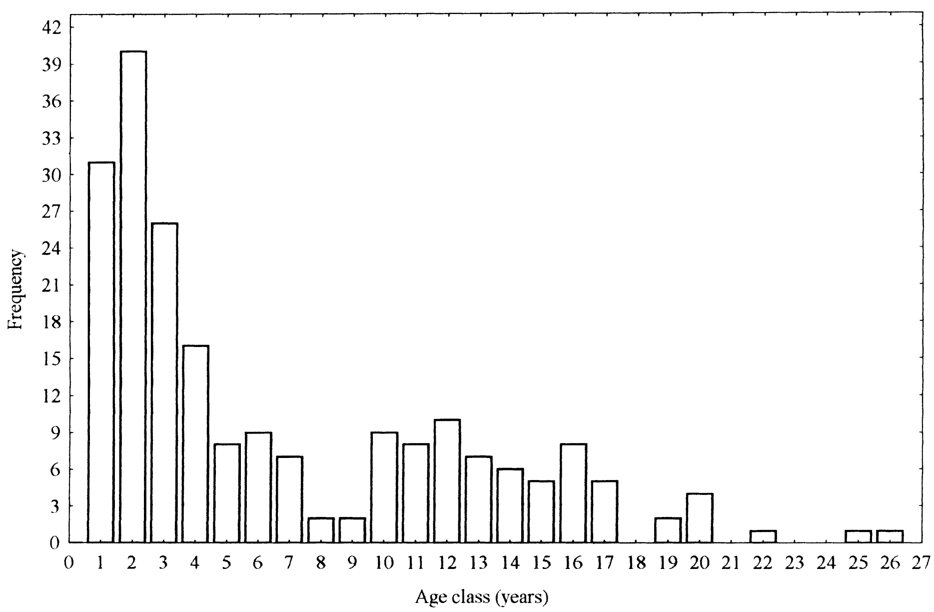

Fig. 3. Age frequency distribution of *G. buergeri* in the 100–200 m depth zone off the Pilbara coast of north-western Australia

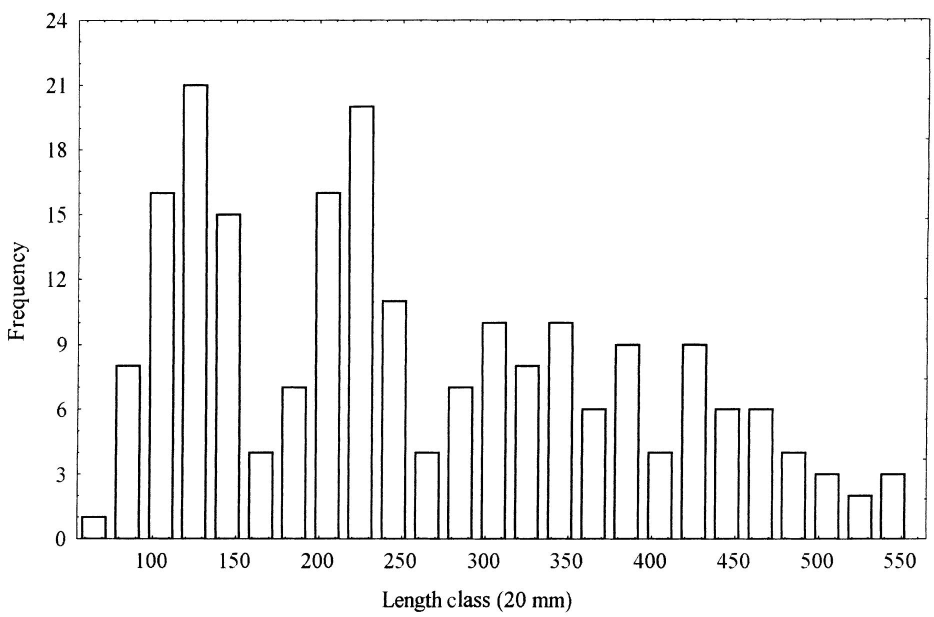

Fig. 4. Length frequency distribution of *G. buergeri* sampled for age determination (10 mm length classes)

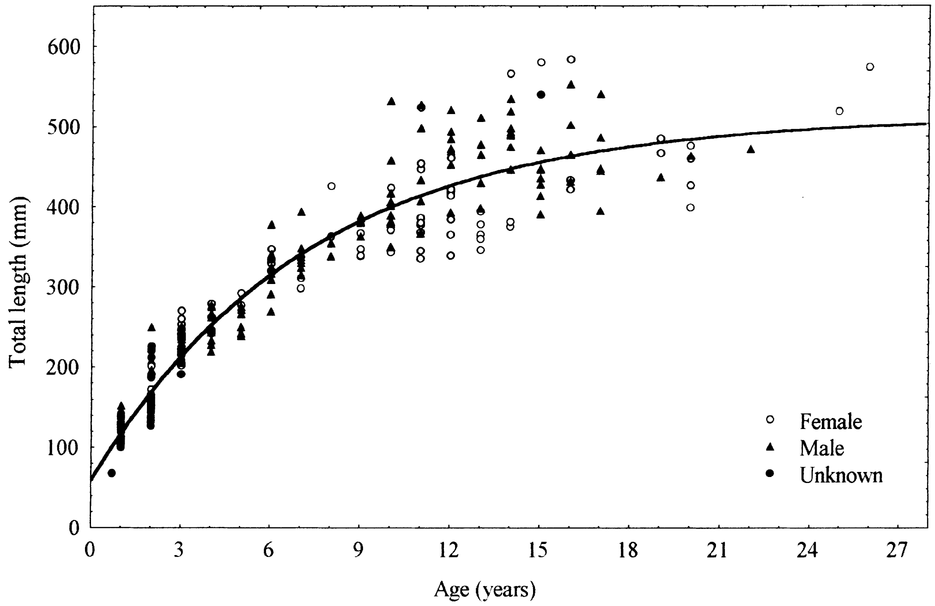

Fig. 5. Von Bertalanffy length-at-age growth curve for *G. buergeri* off the Pilbara coast of north-western Australia

Table 4
Growth parameters calculated from the von Bertalanffy growth function ($L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$) and means, minima and maxima of total length and age, where the length is TL (mm) and age (t) is in years for *G. buergeri* from the Pilbara coast of Western Australia (n = sample size)

Parameters	Male	Female	Total
n	181	145	256
L_∞	528.3	501.8	512.7
K	0.137	0.136	0.139
t_0	−0.78	−0.99	−0.89
r^2	0.940	0.915	0.911
n	111	76	257
TL_{mean}	369.7	349.2	304.3
TL_{min}	152	151	68
TL_{max}	553	584	584
n	111	75	256
t_{mean}	9.40	9.59	7.39
t_{min}	1	2	0.7
t_{max}	22	26	26

(Table 4). The VBGF indicates that the rate of growth of *G. buergeri* decreases slowly with increasing age. Growth of *G. buergeri* is slow, with growth in length of age classes beyond 10+ much reduced. Length-at-age of *G. buergeri* was not significantly different between sexes (P > 0.05; Fig. 5).

Glaucosoma buergeri less than 2+ years of age were not fully recruited to the sampled population and were excluded from the mortality estimates derived from catch curves (Fig. 6). The estimated M of the Pilbara population of *G. buergeri* was estimated to be 0.14 ($r^2 = 0.84$, ages 2–26 years), representing an annual survivorship of approximately 87% per year (Table 5). Individuals in the 8+ and 9+ age classes were not well represented in the catch (Fig. 3) and were excluded from the catch curve as they do not appear to have recruited in similar numbers to other cohorts (the equilibrium assumption). However, the descending right-hand limb of the catch curve fits well across most ages and hence M was assumed to be constant.

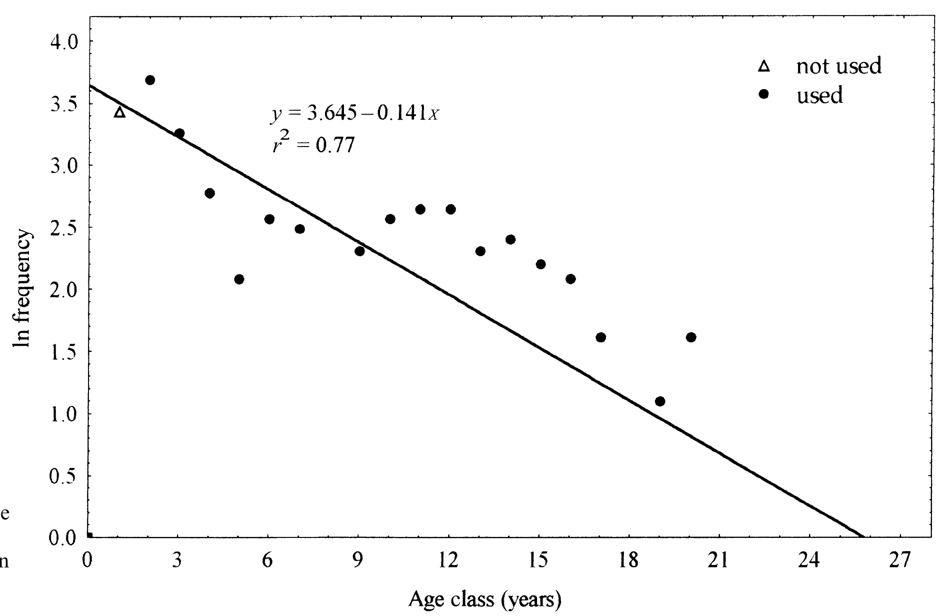

Fig. 6. Catch-curve for *G. buergeri* in the 100–200 m depth zone off the Pilbara coast of north-western Australia based on counts of annuli in sectioned otoliths (sagittae)

Table 5
Estimates of natural mortality (M) and survivorship (S) for *G. buergeri* derived from catch curves based on ages determined from sectioned otoliths, and from the empirical regression equations of Hoenig (1983) and Pauly (1980). The limit reference point, F_{limit} (Patterson 1992) is derived based on estimates of M from catch curves

Parameter	Catch curve	Hoenig estimate	Pauly estimate
M	0.140	0.160	0.221
S	86.9%	85.2%	80.2%
F_{limit}	0.094		

Estimates of M from the equation of Hoenig (1983) were similar to those derived from catch curves (Table 5). The estimate of M from the equation of Pauly (1980) was to some extent higher than that derived from both the catch curve and the Hoenig (1983) equation (Table 5).

Limit reference point estimation

The value of F_{limit} for *G. buergeri* was estimated to be 0.094 (Table 5), indicating that less than 10% of the available stock can be harvested on an annual basis.

Discussion

This study is the first to establish the demographic parameters of age, growth rate and mortality of *G. buergeri*. Sagittae of *G. buergeri* were found to have a distinct pattern of alternating translucent and opaque (annuli) bands. Under reflected light on a black background annuli appear opaque in contrast to surrounding translucent areas. The first few annuli are usually broad and diffuse, with subsequent annuli becoming progressively more compact towards the edge of the otolith. Although the otoliths of *G. buergeri* are interpretable, there is a large amount of individual variability and some otoliths were difficult to assess.

Evidence of the annual basis of ring formation is important in any age and growth study using calcareous structures such as otoliths to determine age. The presence of annuli in *G. buergeri* in this study has not been directly validated. However, a large amount of literature has largely confirmed the hypothesis of annuli in otoliths of both temperate and tropical fishes (e.g. Secor et al. 1995; Fowler 1995) and it has been clearly demonstrated that the alternating bands of opaque and translucent zones found in the sectioned otoliths of fish sampled in similar latitudes on the Great Barrier Reef represent annuli (Fowler and Doherty 1992; Ferreira and Russ 1992, 1994; Newman et al. 1996; Hart and Russ 1996; Choat and Axe 1996; Cappo et al. 2000). No studies have clearly disproved that growth rings in sectioned otoliths are not annuli.

Furthermore, evidence of the presence of annuli can be assessed by a number of criteria (Fowler and Doherty 1992). Otoliths must display an internal structure of increments. Otoliths must grow throughout the lives of the fish at a perceptible rate and there must be a positive relationship between the size of fish caught and the size of the otoliths. The internal structure of increments must be formed periodically on a regular time scale (e.g. once per year). Several observations confirm the use of sectioned otoliths to age *G. buergeri*. Transverse sections of sagittae showed a pattern of alternating translucent and opaque zones. The alternating bands of opaque and translucent zones considered as annuli in this study are analogous to those reported as annuli in other species by Fowler and Doherty (1992), Ferreira and Russ (1994), Choat and Axe (1996), Hart and Russ (1996), Newman et al. (1996, 2000), and Cappo et al. (2000). There was a strong correlation between otolith weight and fish age ($r^2 = 0.912$) and the length-at-age of fish increased as the number of rings (ages) increased. The high correlation obtained between otolith weight and fish age further supports the suggestion that the bands reported in this study are formed on an annual basis. The strong correlation between otolith weight and fish age indicates that otolith weight may be used as a proxy for fish age and afford a cost effective and non-subjective method of age determination for fishery management purposes.

The oldest fish sampled in this study was a female 26 years of age, and reflects the present maximum observed longevity for this species. Growth in length of *G. buergeri* is slow ($K = 0.139$) throughout their life with asymptotic length being achieved late in life. Approximately 40% of growth to L_∞ is accomplished within the first 3 years of their lifespan, with approximately 75% of growth to L_∞ accomplished within the first 9 years of life. Growth in length is much reduced after 12 years of age. The range of fish size and age used in age and growth studies may influence estimates of the von Bertalanffy growth equation if they are not representative of the population. This growth study was considered comprehensive because specimens were obtained across a broad size range (68–584 mm), with large quantities of small fish (< 200 mm) collected from trawl catches.

Estimating mortality using age-based catch curves involves a number of assumptions. These include the assumptions of constant recruitment and constant mortality for each age class. The steady-state or equilibrium assumption of constant recruitment is likely to be violated for most species as recruitment can be variable and inconsistent (e.g. Doherty and Fowler 1994). However, catch curves are reliable and robust if a large number of age classes are included within the sample and no trend in recruitment is evident. The catch curve of *G. buergeri* suggests that the mortality rate across each age class is relatively constant and therefore the natural mortality rate estimated from the catch curve of *G. buergeri* is likely to be robust. *Glaucosoma buergeri* were fully recruited to the fish trawl fishery by age 2, and the instantaneous rate of natural mortality is low ($M = 0.14$). Low rates of natural mortality were expected, given the long life span of *G. buergeri*.

The M derived from the age structure of *G. buergeri* was compared to those derived from the empirical regression techniques of Hoenig (1983) and Pauly (1980). Hoenig's (1983) empirical equation, based on maximum observed age provided similar estimates of M to those derived from catch curves. The estimates of M obtained from the regression equation of Pauly (1980) provided a slight overestimate of M compared with the catch curve estimate for these fishes.

However, the Pauly (1980) equation is influenced by the estimates used for mean annual water temperature. In this study sea surface temperature is used as a proxy because the water temperature in the 100–200 m depth zone was not known. Reducing the value for water temperature reduces the estimate of M. Therefore, in this study the Pauly (1980) equation may provide a similar measure of M to the other methods if a more reliable estimate of water temperature can be provided for the deepwater zone off the Pilbara coast. Caution is therefore recommended in the use of empirical equations for the calculation of M as errors in estimates of

M have profound fisheries management implications as yield and production models all require estimates of M. Overestimates of M provide a misleading impression of the potential yield of fish stocks and this may lead to overexploitation.

The low age at full recruitment to the fish trawl fishery and the ability of trawl fishers to catch juveniles of this species indicate that *G. buergeri* is highly vulnerable to capture by the fish trawl fishery and is therefore susceptible to overfishing. High effort levels within localized areas are likely to rapidly deplete local fish populations.

Glaucosoma buergeri off the Pilbara coast of Western Australia are long-lived (to at least 26 years of age), slow-growing fish, with low rates of natural mortality. These life-history characteristics indicate that these fish have a low production potential and are vulnerable to over-exploitation. This is reflected in the low limit reference point (F_{limit}) estimated by this study, which indicates that less than 10% of the available population can be harvested on an annual basis. Furthermore, the vulnerability of juvenile fish to capture by fish trawl nets results in a reduction of the available yield to the fishery for this species.

The age estimates and growth parameters obtained during this study will assist in the development of age-based stock assessment models for this species. Fishery managers need to ensure that fishery management plans maintain adequate egg production and hence recruitment to both safeguard and promote the sustainable utilisation of the *G. buergeri* resource. Spatial area closures for protection of both the spawning stock biomass and areas of high juvenile recruitment are recommended for this species.

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