

Size compositions and reproductive biology of an important bycatch shark species (*Heterodontus portusjacksoni*) in south-western Australian waters

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Heterodontus portusjacksoni was obtained from the catches of commercial trawl, gillnet and longline fisheries operating in south-western Australian waters, in which this shark is an abundant bycatch species. Ninety per cent of the *H. portusjacksoni* caught by commercial trawling in a marine embayment were <400 mm in total length, whereas 99 and 100%, respectively, of the individuals taken by commercial gillnet and longline outside that embayment were >400 mm. Although the differences between the size compositions in the catches obtained by trawling vs both gillnetting and longlining, which were similar, are partly attributable to gear selectivity, they also reflect a use by juvenile *H. portusjacksoni* of protected nearshore waters as nursery areas and a tendency for larger juveniles and adults to occupy reef/rock habitats in a range of water depths. The fact that all but one of the numerous *H. portusjacksoni* >800 mm were females is reflected in the ratio of females to males differing significantly from parity in the gillnet and longline samples. Yolked oocytes usually take one year to develop to ovulatory size. Ovulation occurs in late winter to early summer and hatching takes place a year later when the embryo is 180–220 mm. The claspers of males commence rapid growth at a total length of ~450 mm, coincident with the onset of clasper calcification and gonadal maturation. The rate of clasper growth relative to total length reached a maximum at ~570 mm and then declined precipitously as the claspers approached full calcification. Based on gonadal criteria, the L_{50} at maturity for females (805 mm) was nearly 40% greater than that for males (593 mm). Values of the deviance information criterion and marked overlap in their 95% confidence intervals demonstrate that the L_{50} of 581 mm derived for males using full clasper calcification as the index of maturity was equally valid as the above L_{50} derived for males at maturity using gonadal criteria. The capture of substantial numbers of juveniles by trawling and of females < L_{50} at maturity by gillnetting and longlining may be having localized effects on the population structure of *H. portusjacksoni* in south-western Australian waters.

Keywords: Port Jackson shark, habitats, ovulation, sex-ratios, size at maturity, clasper growth

Submitted 25 January 2007; accepted 23 November 2007

INTRODUCTION

Sharks are particularly vulnerable to over-exploitation by fishing because they have low fecundities, mature late and live for long periods (Stevens *et al.*, 2000; Musick, 2004). Consequently, the problems posed to marine ecosystems by removing sharks through fishing are becoming increasingly recognized by fisheries and environmental managers. The targeting of some shark species has been so severe that it has led to the collapse of the stocks of those species (e.g. Stevens *et al.*, 2000; Musick, 2004; Ellis *et al.*, 2005). Furthermore, commercial fishing can lead to the capture and mortality of large numbers of certain shark species that constitute part of the bycatch (Stevens *et al.*, 2000; Stobutzki *et al.*, 2002). Data on crucial aspects of the biology of such bycatch species are thus required by managers to facilitate their development of plans for ensuring the sustainability of the populations of these species and thus also of the ecosystems of which they

are a part. Such data include the size compositions and sex ratios of catches by each fishing method, the habitats occupied, the length at maturity and certain aspects of their reproductive biology.

The Port Jackson shark *Heterodontus portusjacksoni*, which is endemic to the temperate waters of Australia south of ~28° S (Last & Stevens, 1994), is abundant in the catches of certain fisheries in south-western and south-eastern Australia (McAuley & Simpfendorfer, 2003; Walker, 2005). In south-western Australia, it was the most numerous of the bycatch fish species and the fourth most abundant fish species overall in the catches of the demersal gillnet and longline fisheries of these waters between 1994 and 1999 (McAuley & Simpfendorfer, 2003). Furthermore, the juveniles of *H. portusjacksoni* are a major component of the bycatch of the inshore prawn trawl fishery of the lower west coast of Australia.

Despite the abundance of *H. portusjacksoni* in the commercial catches of the inner-shelf demersal fisheries of southern Australia, there have been few detailed studies of the biology of this or any other of the nine species of the Heterodontidae, a family widely distributed in the Indian and Pacific Oceans (Compagno *et al.*, 2005) and the only

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shark family in which all species exhibit single (external) oviparity (Musick & Ellis, 2005). Tagging and underwater observations demonstrated that, in eastern Australia, the females of this species migrate inshore in winter to deposit their eggs, and that they and their males exhibit, at that time, a high level of site fidelity (McLaughlin & O'Gower, 1971; O'Gower, 1995). These characteristics, together with the low fecundity, late maturity and longevity of sharks in general, make this species potentially susceptible to the effects of local fishing and to the impacts of any changes to their near-shore habitats. The study by Tovar-Avila (2006) provided data on aspects of the biology of three populations of *H. portusjacksoni* in south-eastern Australia. However, as recognized by that author, that study was based predominantly on the large individuals that were caught by commercial fishing and thus the resulting maturity ogives for the different regions may have been influenced by differences in the types of fishing gear used in the different regions.

A full size-range of *H. portusjacksoni* was obtained at regular intervals from the catches of commercial trawl, gillnet and longline fisheries operating in different areas and water depths off the south-western Australian coast to provide data that would enable us to undertake the following: (1) determine, through comparing the size compositions of the females and males in the full range of catches, the habitats occupied by the juveniles and adults and thus whether they differ; (2) determine whether the sex ratios in the samples obtained using the three fishing methods differ and, if so, consider the implications of these differences; (3) elucidate details of the reproductive cycle, including the pattern of oocyte development, the timing of ovulation and hatching, and the size at hatching; (4) describe quantitatively the pattern and rate of growth of claspers in relation to total length; (5) use gonadal data to determine the L_{50} s of females and males at maturity, i.e. the lengths at which 50% of those sexes in the population attain maturity; and (6) test the hypothesis that the L_{50} derived using full clasper calcification as the index of maturity for males is essentially the same as that derived using gonadal data. Our suite of results is compared with those obtained elsewhere for *H. portusjacksoni* and for other oviparous shark species, and the data on size compositions and the L_{50} at maturity are used to ascertain the extent to which *H. portusjacksoni* is caught by each method before individuals have had the opportunity to reproduce.

MATERIALS AND METHODS

Sampling regime, measurements and gonadal maturity stages

A total of 514 *H. portusjacksoni* was collected from the bycatch of commercial fishing vessels operating in south-western Australian waters between 31° S on the west coast and 118° E on the south coast. Commercial fishing involved the following: (1) otter trawling for prawns or scallops in water depths of mainly 8–13 m in a large marine embayment (Comet Bay) that contained substantial areas of bare sand and sea grass (predominantly *Posidonia* spp. and *Amphibolis antarctica*). Trawling was conducted at ~6.5 km h⁻¹ using a mesh of 45 mm in the codend; (2) gillnetting for sharks in water depths of 24–73 m and using up to 7000 m of net

with a mesh size of either 165 or 178 mm; and (3) longlining for sharks in water depths typically of 65 to 73 m and employing ~6400 m of line with ~360 hooks. The main shark species targeted by these demersal gillnet and longline fisheries are *Mustelus antarcticus*, *Carcharhinus obscurus* and *Furgaleus macki* (McAuley & Simpfendorfer, 2003). A further 41 individuals were obtained opportunistically by our own line fishing in the same areas to provide additional reproductive data for those few months when commercial fishing was limited and sample sizes were therefore small. Samples were obtained at monthly to three-monthly intervals between November 2002 and November 2006 and yielded individuals for all calendar months of the year. Because the data for the different variables in any one year were limited, and as plots of the raw data indicated that each variable followed similar trends among years, the data for the corresponding calendar months were combined.

The sex of each *H. portusjacksoni*, and its total length (to the nearest 1 mm) and generally also weight (to the nearest 1 g), were recorded. The weight of the right (functional) ovary of females and the collective weight of both of the testes of males were recorded to the nearest 1 g. The outer length of the right clasper of each male, i.e. distance between its distal tip and point of insertion in the pelvic fin, was measured to the nearest 1 mm and the extent of calcification of each clasper, i.e. whether it was non-calcified, partially calcified or fully calcified, was recorded.

In the vast majority of cases, the gonads of female and male *H. portusjacksoni* were able to be assigned a maturity stage using the criteria outlined by White *et al.* (2001). For females, Stage 1 = uteri small and thin and oocytes not macroscopically visible. Stage 2 = uteri enlarging but still thin and oocytes becoming visible but not yet containing yolk. Stage 3 = uteri enlarged and oocytes yolked. Stage 4 = pregnant and Stage 5 = uteri or cloaca distended, indicating that oviposition has recently occurred. For males, the maturity stages based on gonadal criteria are as follows: Stage 1 = seminal vesicles small and thin and testes not well defined; Stage 2 = seminal vesicles enlarging and starting to become coiled, but testes not yet lobed; Stage 3 = seminal vesicles are tightly coiled and testes lobed; and Stage 4 = similar to Stage 3, but with semen present in distal portion of seminal vesicle. Females and males with gonads at Stages 1 and 2 cannot reproduce and are therefore immature, whereas those at Stages 3 and 4 and, in the case of females, also Stage 5, can potentially reproduce, or have reproduced, and are therefore regarded as mature. When employing clasper criteria as an indicator of maturity, males with non-calcified and partially-calcified claspers are incapable of copulation and are thus regarded as sexually immature, while those with fully-calcified claspers have the ability to copulate and are thus regarded as mature.

Reproductive cycle and clasper development

The gonadosomatic index (GSI) was determined from the equation $W_1/W_2 \times 100$, where W_1 = weight of right (functional) ovary for females and the weight of both testes in males and W_2 = total body weight. The monthly GSIs for female *H. portusjacksoni* were replicated to simulate three consecutive years of data and, employing a span of 0.3, which produced an adequate level of smoothing, then smoothed using the loess function within R (Ihaka &

Gentleman, 1996). As this approach failed to provide an adequate representation of the male GSIs, the loess curve was fitted to the monthly GSIs for only a 12 month period and employing a span of 0.9.

The number of oocytes in the right (functional) ovary of each female, which macroscopically could clearly be seen to have become yolked (diameters >10 mm), was recorded, and the diameter of the largest of those oocytes was measured to the nearest 1 mm. As two distinct size-classes of yolked oocytes were often present in the ovary, the number of yolked oocytes in the smaller of those size-classes and the diameter of the largest of those oocytes were also recorded. The yolked oocytes were then assigned to one of two categories, i.e. large oocytes (>25 mm diameter) or small oocytes (<25 mm diameter) on the basis that a diameter of 25 mm demarcated the large and small yolked oocytes in a plot of the monthly maximum oocyte diameters (MODs) (see Results).

The monthly numbers of the groups of both large and small oocytes were replicated to simulate three consecutive years of data and then, employing an appropriate span of 0.25, smoothed using the loess function within R (Ihaka & Gentleman, 1996).

The MODs for the mature females in each month were described empirically by a mixture of five identical generalized logistic curves representing oocytes in 'cohorts' $j = -2, -1, 0, 1$ and 2. The equation for curve j was

$$\hat{M}_t = M_{\min} + (M_{\max} - M_{\min}) \times \left\{ 1 + \exp \left[-\log_e(19) \frac{t - (t_{50} - j)}{t_{95} - t_{50}} \right] \right\}^{-1} \quad (1)$$

and represents the expected growth of the MOD at time t within the year from its minimum value, M_{\min} , to its maximum, M_{\max} , with the point of inflection at $t_{50} - j$ (years) relative to the start of the year and with the value of \hat{M}_t attaining 95% of the total growth range at t_{95} years relative to the start of the year. The times of inflection of the successive curves in the mixture were separated by one year, with two curves on either side of the central curve. Two oocyte development periods were considered, i.e. annual ($T = 1$ y) and biennial ($T = 2$ y), and ovulation was assumed to occur over a period determined by a second logistic function, where the probability of ovulation for oocytes in cohort j by time t relative to the start of the year was calculated as $g_{t,j} = \{1 + \exp[-\log_e(19)(t - (t_{50} + 0.5T - j))/d]\}^{-1}$. The proportion of oocytes in curve j at time t may be calculated as $\pi_{t,j} = g_{t,j}h_{t,j} / \sum_{j=-2}^2 g_{t,j}h_{t,j}$ where $h_{t,j} = 1 - \{1 + \exp[-\log_e(19)(t - (t_{50} - 0.5T - j))/d]\}^{-1}$ represents the proportion of oocytes that have commenced development. A further case was also considered, in which oocyte development was assumed to occur over one year, but with a fraction f of the female sharks possessing oocytes that failed to develop during the year and thus with MODs remaining at M_{\min} , thereby adding an additional component to the mixture of oocyte diameters and with the values of $\pi_{t,j}$ being modified accordingly. Observed values of M at time t were assumed to be normally distributed with a common variance σ^2 around the expected value for the curve with which the observation is associated. Estimates of t_{50} , t_{95} , M_{\min} , M_{\max} , σ and, where appropriate, f , were obtained by maximizing the likelihood of the data $\lambda = \sum_{i=1}^n \sum_{j=-2}^2 \pi_{t,j} \phi_{i,j}$ where $\phi_{i,j} = (1/\sqrt{2\pi\sigma^2}) \exp [-(M_i -$

$\hat{M}_i)^2/2\sigma^2]$. As, during exploration of results, estimates of d obtained from maximum likelihood were found to be not feasible, d was set to 0.4 years, a value found to produce realistic results. Values of the Akaike information criterion (AIC) were calculated as $AIC = -2\log_e(\lambda) + 2K$, where K is the number of parameters estimated (Burnham & Anderson, 2002). The Akaike difference for model i of each of the three candidate models was then calculated as $\Delta_i = AIC_i - AIC_{\min}$ and from this the Akaike weight, i.e. weight of evidence supporting this model, was determined as $w_i = \exp(-0.5\Delta_i) / \sum_{r=1}^3 \exp(-0.5\Delta_r)$ (Burnham & Anderson, 2002).

A model describing the relationship between clasper length (CL) and total length (L) of males was explored, i.e. $CL = aL^b(1 - G_L) + CL_{\max}G_L$, where $G_L = \{1 + \exp[-\log_e(19)(L - L_{50}^{CL})/d]\}^{-1}$. Based on the data, it was assumed that an allometric relationship $CL = aL^b$ exists before the claspers commence rapid growth and calcification. Subsequent growth of the claspers is logistic during the period when it is partially calcified and ceases when the claspers become fully calcified.

The model was fitted in two phases. First, estimates of the parameters of the allometric relationship, a and b , and their standard errors, were obtained using WinBUGS (Lunn *et al.*, 2000) by fitting the allometric relationship $CL_L = aL^b$ to the data for those males with non-calcified claspers. For this, it was assumed that the observation errors of CL were normally distributed with constant variance over the range of lengths. Non-informative prior probability distributions were imposed, with those for a and b being normal distributions and that of the precision of the observation errors (t) being a gamma distribution. Appropriate levels of burn-in (1000 iterations) and thinning (4000 iterations) were determined by testing a preliminary output from WinBUGS using the Raftery & Lewis procedure (Raftery & Lewis, 1992) in Bayesian Output Analysis (BOA) (Smith, 2005), which was run within R (Ihaka & Gentleman, 1996) and the model was then run through WinBUGS for a total of 1100000 iterations.

The resulting estimates of a and b , and their standard errors, were then inserted as prior probability distributions into a second WinBUGS analysis of the full data set, i.e. data for males with non-calcified, partially-calcified and fully-calcified claspers. The prior probability distributions of the parameters CL_{\max} , L_{50}^{CL} and d were assumed to be normal, while that of τ was assumed to be a gamma distribution. All prior distributions other than for a and b were non-informative. The required levels of burn-in and thinning for convergence were assessed using the BOA procedure in R. WinBUGS was then run for a total of 60000 iterations, with a burn in of 1000 iterations and thinning of 20 iterations, to determine estimates of the parameters a , b , CL_{\max} , L_{50}^{CL} , d and τ and of the predicted values of CL at different values of L .

Estimates of the rate of change of clasper length with increasing total length were obtained by calculating values of $\Delta CL/\Delta L = (CL_{L+\Delta L} - CL_L)/\Delta L$ over a range of values of L with $\Delta L = 0.1$ and employing the mean values of the parameters determined from the WinBUGS analysis.

Length at maturity

The lengths at which 50% of the females and males reach maturity (L_{50}) were estimated using WinBUGS and employing, as criteria for maturity, gonadal maturity status

(stages ≥ 3) for both females and males and also full clasper calcification for males. The probability (P) that an individual of total length (L) is mature was estimated as $P = \{1 + \exp [-(\alpha + \beta L)]\}^{-1}$, where α and β are parameters that determine the location and shape of the logistic curve. The parameters α and β were transformed to a form more meaningful to biologists, namely the lengths L_{50} and L_{95} by which 50 and 95% of fish have attained maturity, respectively, using the equations $L_{50} = -\alpha/\beta$ and $L_{95} = [\log_e(19) - \alpha]/\beta$. These parameters, i.e. L_{50} and L_{95} , correspond to the lengths at which P equates to the values 0.5 and 0.95, respectively. The equation thus becomes $P = \{1 + \exp [-\log_e(19)/(L - L_{50})/(L_{95} - L_{50})]\}^{-1}$.

The analysis was undertaken using WinBUGS (Lunn *et al.*, 2000) and assumed that the maturity status recorded for each shark, i.e. immature or mature, was the outcome of a Bernoulli trial in which the probability of the shark being mature was the value of P calculated by substituting the length of the shark L into the above logistic equation. Non-informative, normal distributions were used as the prior probability distributions of the parameters L_{50} and L_{95} . Appropriate levels of burn-in and thinning factors to assure convergence were determined by testing a preliminary output from WinBUGS using the procedure of Raftery & Lewis (1992) in BOA (Smith, 2005), which was run within R (Ihaka & Gentleman, 1996). WinBUGS was then run for 1100000 iterations, with a burn in of 250 iterations and thinning of 300 iterations, to determine estimates of the parameters and of the predicted values of the estimated P at different lengths. The logistic curves for females and males were compared by examining the value of the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002) calculated with WinBUGS using a single logistic curve for both females and males and comparing this with the value obtained using separate curves for each sex. The same procedure was applied to compare the logistic curves derived for males using gonadal and clasper criteria as indices of maturity.

RESULTS

Length compositions by fishing method and implications for habitat use

The lengths of the 548 *H. portusjacksoni* collected from commercial fishers and by opportunistic sampling ranged from 209–1300 mm for females and 180–815 mm for males (Figure 1). They thus covered lengths ranging from those at which hatching occurs to one above which this species is rarely found (Compagno, 2001). The weights of females and males ranged from 39 to 10600 g and from 39 to 4000 g, respectively. Twenty-nine of these individuals were neonates, i.e. recently-hatched individuals which still possessed a yolk stalk or the internal remnant of the yolk sac and an umbilical scar. Their lengths ranged from 180–220 mm, with a mean of 212 mm and 95% confidence limits of 208–216 mm.

The length–frequency distribution for females was trimodal, with modal length-classes at 200–249, 650–699 and 900–949 mm, while that for males was bimodal, with the two modal length-classes being the same or very similar to the first two modal length-classes in the length–frequency distribution for females (Figure 1). The mean length of females

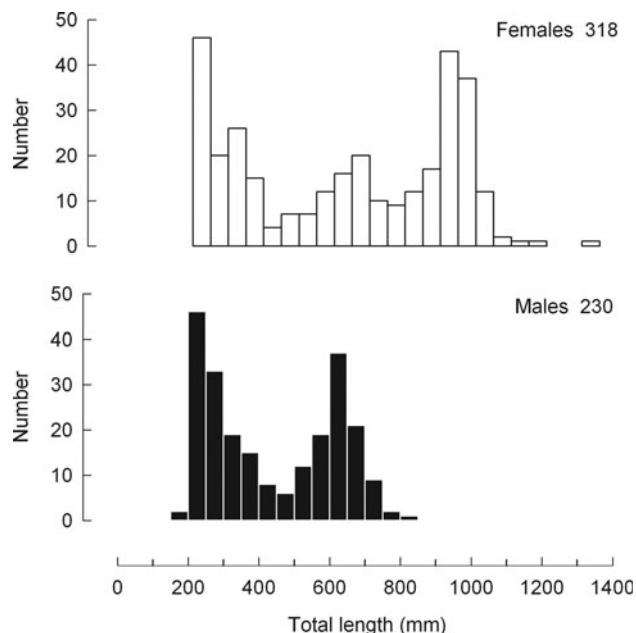


Fig. 1. Length–frequency distributions for females and males of *Heterodontus portusjacksoni* in samples obtained by all methods.

(635 mm) was far greater than that of males (440 mm) and all 123 fish with lengths >815 mm were females.

The length–frequency distribution for *H. portusjacksoni* caught by otter trawling differed markedly from those obtained by both gillnet and longline, which were similar (Figure 2). Thus, the vast majority of fish (90%) caught by trawling were <400 mm in length, whereas virtually all of those caught by gillnetting (99%) and all longlining were >400 mm. The length compositions of all *H. portusjacksoni* collected by commercial gillnetting and longlining from water depths of 24–45 m were essentially the same as those caught by the same methods in water depths of 55–80 m. Three additional gillnet sets and four longline sets in water depths of 80–104 m yielded only three *H. portusjacksoni*, which is far less than would be expected to be obtained by a comparable sampling effort in shallower waters.

The sex ratio was significantly influenced by the method of capture ($\chi^2 = 18.20$, $P < 0.001$). The ratio of females to males in the trawl samples, i.e. 1:1.12, was not significantly different from parity ($\chi^2 = 0.40$, $P > 0.05$), whereas it was significantly different from parity in the case of both gillnet samples, i.e. 1:0.69 ($\chi^2 = 5.62$, $P < 0.05$), and longline samples, i.e. 1:0.40 ($\chi^2 = 11.88$, $P < 0.001$). Two hermaphrodites of 924 mm and 706 mm were also present in the longline samples, the first of which was described in Jones *et al.* (2005).

Reproductive cycle and development of claspers

On the basis of the loess curve fitted to the monthly individual GSIs of males, the GSI increased from $\sim 1\%$ in January to a maximum of $\sim 3.1\%$ in May and then declined to $\sim 2\%$ in August and $\sim 1\%$ in December (Figure 3A). The comparable curve for females shows that the GSI of this sex peaked later, i.e. $\sim 6.0\%$ in August, but likewise declined to its minimum ($\sim 2.3\%$) in December/January (Figure 3B). Although this trend was reflected by that exhibited by the

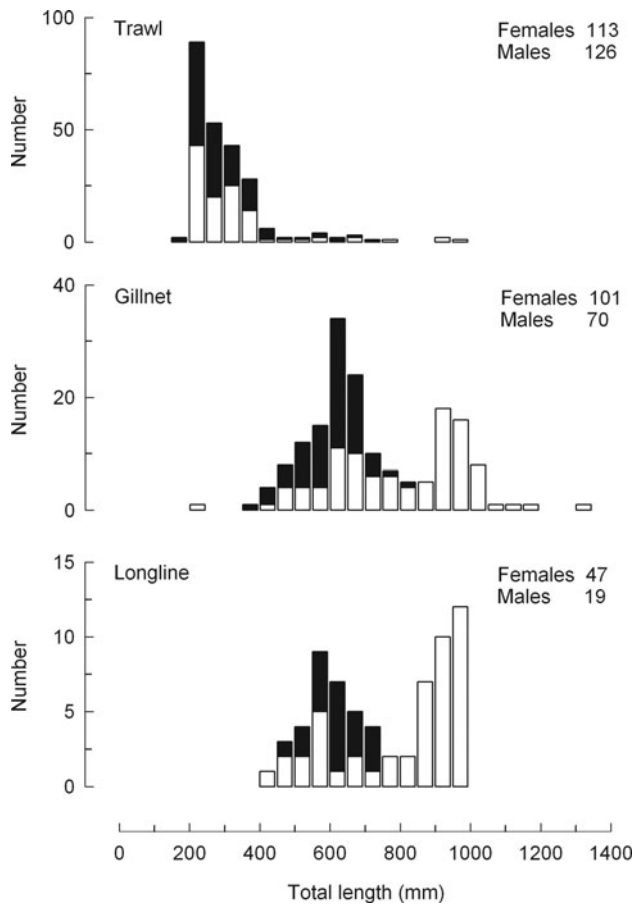


Fig. 2. Length–frequency distributions for females (white histograms) and males (black histograms) of *Heterodontus portusjacksoni* caught by commercial otter trawling, gillnetting and longlining.

maximum values for the GSIs in each month, females with low GSIs of ~1% were present throughout the year.

The loess curve fitted to the monthly numbers of large yolke oocytes (diameter >25 mm) rose to ~15 in February, remaining at about this level until August, before declining precipitously to its minimum in October to December. On the basis of the distribution and number of large oocytes from May to August, the fecundity of 24 *H. portusjacksoni* was estimated as ranging from 9 to 27, with a mean ± 1 SD of 16 ± 5 .

The three models fitted to the monthly MOD values, i.e. those assuming that each group of yolke oocytes take one year, two years or one year with a fraction not developing to ovulation, each describe the data adequately. However, the respective AIC values of 757, 766 and 751 imply that the last of those models provides the best fit (Figure 3D). Furthermore, the values of the Akaike weights provide far stronger support for this last model (95%) than for the one year model (~5%) and the two year model (< 0.1%). The third model indicated that 89% of the yolke oocytes took one year to develop through to ovulation. On the basis of this model, the maximum diameter of yolke oocytes increased from 21 mm in January to 45 mm in August and then tended to level off over the ensuing four months (Figure 3D). The females with only small yolke oocytes (MODs <25 mm) during this period would have represented individuals that had either ovulated all of their large oocytes or whose yolke oocytes had failed to develop to the point of ovulation.

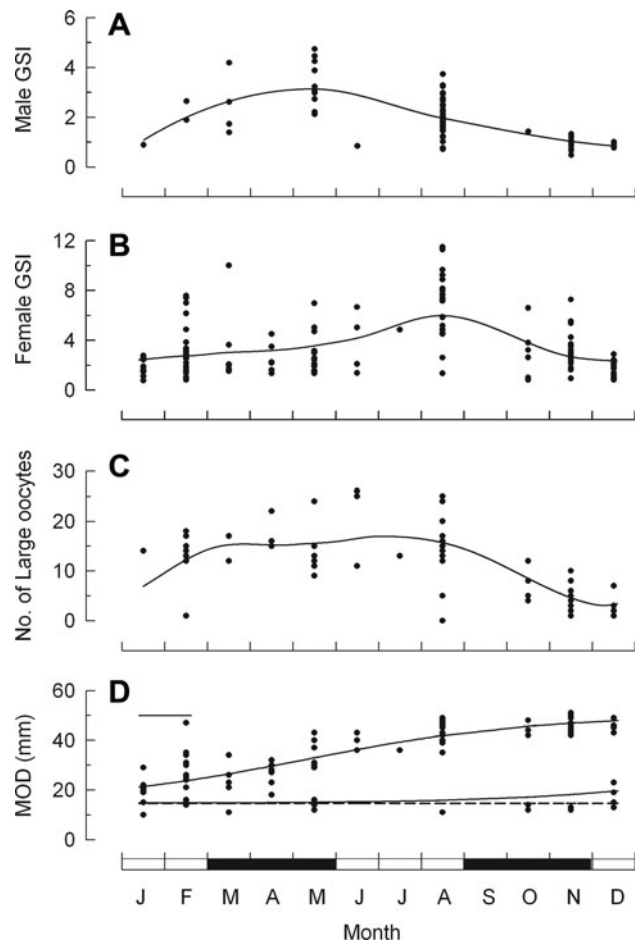


Fig. 3. Monthly individual values for (A) gonadosomatic index of males; (B) gonadosomatic index of females; (C) number of large yolke oocytes, i.e. ≥ 25 mm diameter; and (D) maximum oocyte diameter (MOD) of *Heterodontus portusjacksoni*. A loess curve was used to smooth the points in (A), (B) and (C) and separate lines (solid and dashed) were fitted to the different 'cohorts' of oocytes in (D).

The model provided a very good fit to the clasper lengths vs total lengths of the full size-range of male *H. portusjacksoni* (Figure 4A). The parameters of this model were $a = 0.000067$, $b = 2.02$, $CL_{\max} = 81$ mm, $L_{50}^{CL} = 567$ mm, $d = 94$ mm, $\tau = 0.0119$. The allometric relationship fitted to the clasper length of sharks with non-calcified claspers vs total length emphasizes that, while this male structure remains uncalcified, it increases only slightly as the shark increases in body size (Figure 4A). Thus, the length of uncalcified claspers increased from only 3 to 23 mm over a length-range of 200 to 550 mm. All males with partially-calcified claspers, and which thus represented an intermediate stage in clasper calcification, lay between 429–654 mm and thus around the ascending limb of the logistic element of the model (Figure 4A). The rate of change in clasper length with total length starts to increase rapidly at ~450 mm and peaks at ~570 mm and then decreases rapidly until clasper growth ceases at ~710 mm (Figure 4B).

Length at maturity

On the basis of gonadal criteria, the smallest mature female and male *H. portusjacksoni* were 715 and 595 mm,

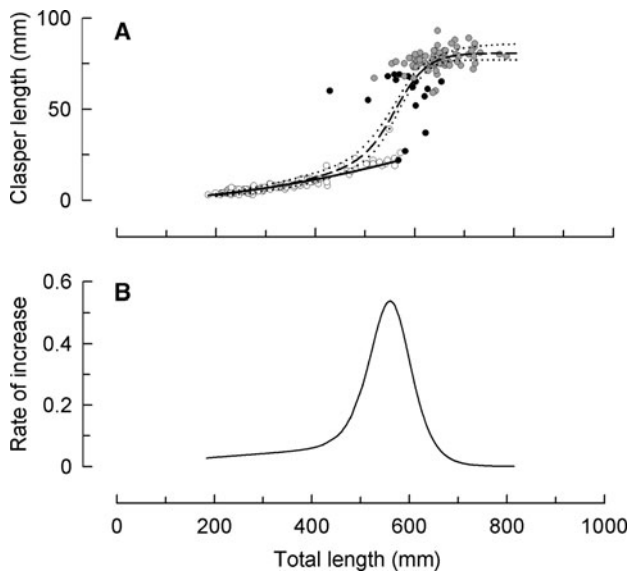


Fig. 4. (A) Modified logistic curve (dashed line) and its 95% confidence limits (dotted lines) describing the overall relationship between clasper length and total length of *Heterodontus portusjacksoni*, and a solid line showing the allometric relationship between the lengths of non-calcified claspers and the total lengths of individuals of this species. White, black and grey circles represent data points for sharks with non-calcified, partially-calcified and fully-calcified claspers, respectively; (B) rate of increase of clasper length relative to total length.

respectively, while the largest immature female and male were 869 and 654 mm, respectively. The percentage of mature females rose from 10% in the 700–749 mm length-class to 50% in the 800–849 mm length-class and was 100% in all length-classes above 900 mm (Figure 5A). With males, the percentage of mature fish rose from 37% in the 550–599 mm size-class to 84% in the 600–649 mm size-class and to 95% by 650–699 mm (Figure 5B). The L_{50} of 805 mm for females at maturity was significantly greater ($P < 0.001$) than the L_{50} of 593 mm for males at maturity (Table 1).

Using the full calcification of claspers as the criterion for maturity, the smallest mature male was 518 mm and the largest immature male was 654 mm. The percentage of males with fully-calcified claspers rose from 8% in the 500–549 mm size-class to 47% in the 550–599 mm length-class to >95% in all classes above 650 mm (Figure 5C). The L_{50} at maturity, derived from the percentages of males with fully-calcified claspers at each length, i.e. 581 mm, differed by only 12 mm from that estimated using the percentages of males with mature gonads at each length. The values of the DIC and the marked overlap in the 95% confidence intervals demonstrated that it would be appropriate to consider either of these L_{50} s as the L_{50} for males at maturity.

DISCUSSION

Size compositions in commercial catches and habitat implications

During this study, multiple sampling methods enabled, for the first time, a full size-range of *H. portusjacksoni* to be collected

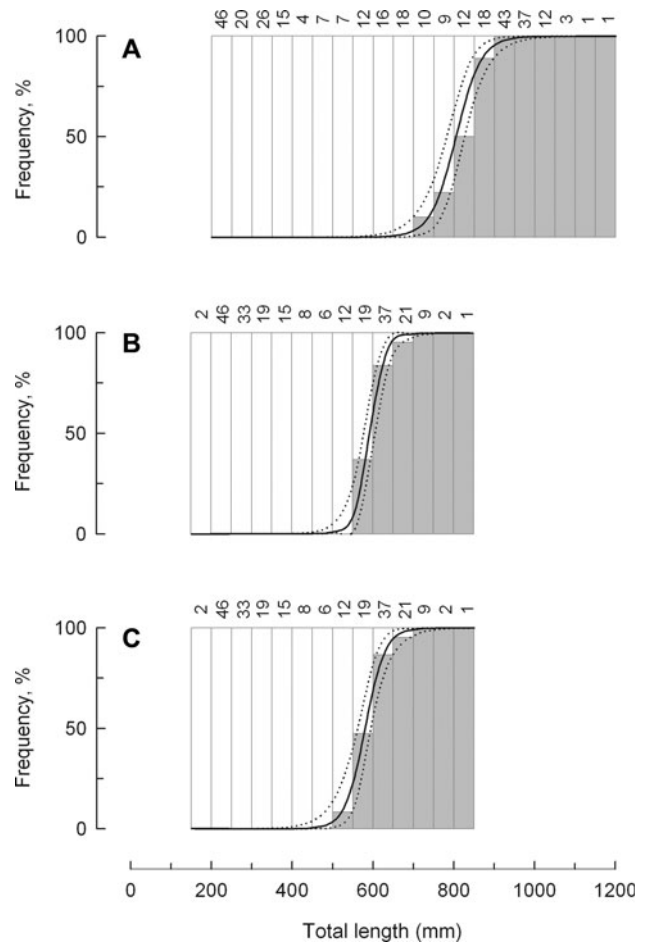


Fig. 5. Percentage frequencies of occurrence of mature *Heterodontus portusjacksoni* in sequential length-classes (grey bars), derived for: (A) females and (B) males from gonadal criteria; and for (C) males using clasper calcification criteria. The logistic curve (solid line), and its 95% confidence limits (dotted lines), relating the probability that an individual is mature to its total length. The number of fish in each 50 mm size-class is shown.

throughout the year from a wide range of depths and over a substantial length of coastline. This facilitated a thorough exploration of the ways in which the size compositions and sex ratios of this heterodontid vary with commercial fishing method and enabled aspects of the reproductive biology of this oviparous species to be elucidated. The length–frequency distribution for *H. portusjacksoni*, derived from samples collected by otter trawl in water depths of 8–13 m in a large marine embayment (Comet Bay) containing areas of bare sand and sea grass, was characterized by the presence of a

Table 1. Estimates of the L_{50} and L_{95} (in mm) for females and males of *Heterodontus portusjacksoni* at maturity and their upper and lower 95% confidence limits. The estimates have been derived using, as an indicator of maturity, gonadal criteria for both females and males and clasper calcification criteria for males.

Parameter (mm)	Female gonads		Male gonads		Male claspers	
	L_{50}	L_{95}	L_{50}	L_{95}	L_{50}	L_{95}
Estimate	805	896	593	647	581	652
Upper	826	931	605	674	594	689
Lower	781	866	579	628	563	629

very strong modal class at 200–249 mm and a paucity of adults. These characteristics contrast strongly with those of the markedly bimodal and similar length–frequency distributions for the gillnet and longline samples collected over reef and rocky substrates in open, offshore waters. Furthermore, the modal length-classes in both the gillnet and longline samples lay at ~600 and 900 mm and thus well to the right of the single modal length-class in the trawl samples. The above differences between the size compositions for the samples obtained by the different gear types are further highlighted by the fact that the vast majority of individuals caught by trawling were <400 mm, whereas the reverse was true for both the gillnet and longline samples.

Although the above differences between the size compositions of *H. portusjacksoni* in the trawl vs both gillnet and longline samples are related to the selectivity of the fishing gear, the capture in a marine embayment of substantial numbers of juveniles, and particularly of their smaller representatives, is consistent with observations of this species in eastern Australia (McLaughlin & O’Gower, 1971). Thus, in those waters, gravid female *H. portusjacksoni* move to inshore reefs where they lay their eggs and the resultant juveniles then use embayments as nursery areas (McLaughlin & O’Gower, 1971). Furthermore, Hutchins & Swainston (1986) noted that areas of sand and weed constitute a major habitat of *H. portusjacksoni* in south-western Australian waters.

Although gillnets and longlines select larger *H. portusjacksoni*, our capture of such individuals in deeper, more offshore waters is consistent with the conclusions drawn by McLaughlin & O’Gower (1971) that, for much of the year, the adults of this species typically occupy this type of environment in eastern Australia. Furthermore, the marked similarity between the length compositions of *H. portusjacksoni* caught by gillnet and longline in a range of water depths along an extensive stretch of coastline strongly suggests that, once *H. portusjacksoni* has left its protected nursery habitats, it does not tend to segregate spatially according to size. Indeed, we found no evidence that this species was abundant in water depths >80 m.

The sharp decline in the descending limb of the length–frequency distribution for the trawl samples from Comet Bay could be due to the larger juveniles of *H. portusjacksoni* moving to deeper water and/or to having a greater ability to evade the trawl net as they increase in size, and/or to fishing-induced mortality. The possibility that juvenile *H. portusjacksoni* are impacted significantly by fishing cannot be excluded as trawling in this embayment occurs virtually every day between late spring and early autumn, and thus when the neonates are present, and it also takes place at night when this species, like *Heterodontus francisci*, is most active (Nelson & Johnson, 1970; McLaughlin & O’Gower, 1971). Furthermore, as the lengths of a substantial proportion of the females of the *H. portusjacksoni* caught by the commercial gillnet and longline fisheries of south-western Australia were less than the L_{50} at maturity, it is possible that, in extensively-fished regions, the numbers of the females of this species that survive to recruit to the breeding stock are being significantly reduced.

Length compositions by sex and sex ratios

The maximum length of 1300 mm for females of *H. portusjacksoni* in south-western Australia was similar to the

maximum recorded for the females of this species in eastern Australia (McLaughlin & O’Gower, 1971) and in the two regions in south-eastern Australia that were sampled by both gillnetting and longlining and thus contained large individuals (Tovar-Avila, 2006). These lengths approximated that beyond which few individuals of this species have been found (Compagno, 2001). However, the maximum length of 815 mm recorded for the males in south-western Australia was far lower than those recorded for the males in the above three regions on the opposite coast of Australia, i.e. ~1000–1100 mm. Thus, whereas the difference between the maximum lengths of females and males was nearly 40% in the south-western Australian population, it was <15% in those other three populations. The latter level of difference parallels more closely the situation in sharks in general as Cortés (2000) found that, on the basis of an analysis of 230 populations representing 164 species of shark, the males of a species were, on average, 10% smaller than their females.

In contrast to the situation in all populations of *H. portusjacksoni* and of sharks in general, the males attained a greater size than their females in the case of the four oviparous species of scyliorhinid studied by Ebert *et al.* (2006) and the same was also true for *Holohalaelurus regani*, another oviparous scyliorhinid (Richardson *et al.*, 2000). However, the males and females of the oviparous hemiscylliid *Chiloscyllium plagiosum* attain a similar length (Chen & Liu, 2006). Thus, among oviparous species, there is no consistent tendency for one sex to grow larger than the other.

The contrast between the similarities in the maximum lengths of the females in all populations of *H. portusjacksoni* and the marked difference in those of their males is reflected in the differences in the structure of the length–frequency distributions for the two sexes in those populations. Thus, for example, the modal length-classes of 200–249, 650–699 and 900–949 mm in the markedly trimodal length–frequency distributions for females in south-western Australia correspond closely with those exhibited by those sexes in eastern Australia (McLaughlin & O’Gower, 1971). Yet, although the length–frequency distribution for males in south-western Australia contained modes in very similar locations as the first two modes for females, it did not contain individuals that produced a corresponding third mode. However, as with females in south-western Australia, the length–frequency distributions for males in the eastern Australian and two south-eastern Australian assemblages (for which there were substantial numbers of large individuals) did contain large males that produced a prominent mode between 900 and 1100 mm (McLaughlin & O’Gower, 1971; Tovar-Avila, 2006). While the modes for the largest males in the latter three populations were located at a slightly smaller length than the modes for their largest females, they are still positioned at a far greater length than even that of the largest individual male (815 mm) in the population from south-western Australia. The presence of the two modes for males and three modes for females in the length–frequency distributions for samples collected from a range of depths along an extensive coastline of south-western Australia strongly suggests that the difference in the size compositions of the two sexes is characteristic of the population in this region as a whole, rather than representing an artefact of sampling. It is not clear what selective pressures led, in south-western Australia, to males being characterized by a far

smaller maximum size than their females and than those of both sexes in south-eastern and eastern Australia.

A combination in both gillnetting and longlining samples from south-western Australia of substantial numbers of both males and females <800 mm, but only of females greater than this length, is reflected in a relatively greater overall number of females than males in those samples. This excess of females contrasts with the situation recorded for juveniles in the samples caught by trawl nets, in which the sex ratio did not differ significantly from parity. Thus, this predominance of females among the larger individuals in south-western Australia is presumably due to a greater longevity of females and/or greater mortality of the two sexes in this region. In contrast to the situation with the south-western Australian population of *H. portusjacksoni*, the sex ratios of three of the oviparous scyliorhinids studied by Ebert *et al.* (2006) and of another oviparous member of that family by Costa *et al.* (2005) were close to parity, whereas males were relatively more abundant than females in the fourth oviparous species of cat shark in the former study, and the females of the oviparous scyliorhinid *Scyliorhinus canicula* were relatively more numerous than their males (Ellis & Shackley, 1997).

Reproductive cycle

The trends exhibited by the monthly MODs provided strong support for the model which indicates that one year is required for the vast majority (89%) of yolked oocytes to develop to the size at which they will be ovulated. Furthermore, the marked decline in the number of large yolked oocytes, and also of the GSIs of females, from high values in August to far lower values in December/January imply that *H. portusjacksoni* ovulates between late winter and early summer, as is the case in south-eastern Australia (Tovar-Avila, 2006). This conclusion regarding the timing of ovulation is consistent with the fact that the five females found with egg cases *in utero* were all caught between August and December. The fact that the GSIs of females peaked in August, rather than in May as with males, suggests that the females store sperm for a period prior to fertilization, as occurs in a number of chondrichthyans (Smith *et al.*, 2004; Walker, 2005; Chen & Liu, 2006).

As ovulation occurs between August and December and all but one of the 29 neonates caught were obtained between August and February, *H. portusjacksoni* in south-western Australia presumably takes approximately a year to develop from a fertilized egg to a fully-developed embryo and hatching, thereby paralleling the situation elsewhere (McLaughlin & O'Gower, 1971; Rodda, 2000). The lengths of neonates, 180–220 mm, were the same as those recorded at hatching in South Australia, but less than the 230–240 mm recorded for eastern Australian populations (McLaughlin & O'Gower, 1971; Rodda, 2000).

From the trends exhibited by reproductive variables, *H. portusjacksoni* belongs to the group of chondrichthyans which Wourms (1977) describes as having a well-defined annual reproductive cycle.

Maturation and size at maturity

The plot shown in Figure 4A demonstrates that, as males of *H. portusjacksoni* increase in total length, the length of their

claspers undergoes the pronounced sigmoidal pattern of growth that has been described for a number of elasmobranchs (e.g. Ebert *et al.*, 2006; White *et al.*, 2006; Marshall *et al.*, 2007). During the initial phase, when the claspers are not yet calcified, the growth is allometric and relatively slow. However, once the claspers commence calcification, their overall rate of growth increases rapidly to reach a peak, as the claspers of some individuals become fully calcified, and then declines markedly to essentially zero when those of all individuals have become fully calcified.

There is a pronounced overlap in the 95% confidence limits for the L_{50} s at which males attain full maturity on the basis of the prevalence of individuals with fully-calcified claspers (581 mm) and fully-mature gonads (593 mm). Thus, the hormonal mechanisms involved in initiating clasper development and gonadal maturation must be closely linked and the L_{50} derived using full clasper calcification can be used as a reliable measure of the L_{50} at maturity. The ability to use the latter L_{50} for maturity in *H. portusjacksoni* parallels the situation recorded by Marshall *et al.* (2007) for the batoid *Trygonorrhina fasciata* and, in such species, allows for the L_{50} of males at maturity to be estimated without having to dissect the animal.

The greater size of females than males of *H. portusjacksoni* at first maturity in south-western Australia parallels the situation with the majority of shark species. Thus, in his review, Cortés (2000) found that this was the case in all but 23 (14.2%) of the 162 species for which there were data. However, it contrasts with the situation in those four species of scyliorhinid studied by Ebert *et al.* (2006) and which, like heterodontids, are oviparous. Yet males of nine of the 17 species of scyliorhinid, which formed part of the review by Cortés (2000), matured at a similar or greater size than their females, and thus, in this family, there is no consistent tendency for either females or males to reach breeding condition at a greater length. However, the L_{50} at maturity is typically greatest in the sex with the greatest maximum length and, in the case of *Chiloscyllium plagiosum* in which the maximum lengths of the males and females were similar, the L_{50} s at maturity of the two sexes, are also similar (e.g. Chen & Liu, 2006).

The marked differences between the maximum sizes attained by the females and males in south-western and south-eastern Australia are paralleled by differences in the L_{50} s at maturity. Thus, the L_{50} for females was 38% greater than that of males in south-western Australia, whereas the corresponding value for the population in south-eastern Australia, for which there was a sufficiently representative sample, was only 23%. This difference suggests that there has been greater selection pressure for a reduction in the L_{50} of males in south-western Australia in association with a reduction in the maximum size of this sex in this region.

ACKNOWLEDGEMENTS

Special thanks are extended to the commercial fishers, and particularly Hugh Gilbert, who helped to obtain samples, and to Alex Hesp for statistical advice and to anonymous referees for their helpful comments and constructive criticisms. Thanks are also extended to friends and colleagues who assisted in sampling and to Terry Walker, Javier Tovar-Avila, Kate Rodda, Rory McAuley and Justin Chidlow for many helpful discussions. Funding for this project was

provided by Murdoch University and the Department of Fisheries, Western Australia.

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