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Demographic analysis of the Port Jackson shark *Heterodontus portusjacksoni* in the coastal waters of eastern Australia

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Abstract. Demographic analyses are used to assess the status and vulnerability of elasmobranchs but their accuracy is often affected by limited basic biological information. Although the Port Jackson shark *Heterodontus portusjacksoni* (Meyer) is currently not considered at threat, there is insufficient data for eastern Australia to assess this rigorously. The present study determined vital demographic rates of adult and juvenile *H. portusjacksoni* at four locations on the central and southern coast of New South Wales, Australia from January 2002 to December 2005 using underwater visual census, tag–recapture and samples obtained from a commercial fishery. Natural mortality was low in adults (0.063–0.074 year^{-1}) and juveniles (0.225 year^{-1}), but substantial at the embryonic stage (0.783–0.896 year^{-1}). Adult growth rates (31.4–32.7 mm year^{-1}) were slightly less than that of juveniles (36.8–37.5 mm year^{-1}). Males at both stages grew slightly faster than females. However, *H. portusjacksoni* had slower growth rates than many other elasmobranch species. Having a low intrinsic rate of increase ($r = 0.069$ year^{-1}), long generation times ($\mu_1 = 22.5$ year) and a low rebound potential, adults are the stage with the greatest impact on population growth. Hence, their life history strategy makes them susceptible to serious decline under exploitation, and management should strive to maintain the adult reproductive stock as a priority.

Additional keywords: conservation, growth rates, matrix models, mortality.

Introduction

Demographic analyses of shark populations first became popular in the 1990s and are now the most widely used population models for this group (Simpfendorfer 2004*a*). Although a wide range of models exist, all rely to some extent on various life history parameters referred to as vital rates that include natural mortality, age at maturity, longevity, growth rates, asymptotic length and fecundity (Jensen 1996; Cortes 2000*b*; Akcakaya 2002; Hall *et al*. 2004). However, in sharks there is a paucity of knowledge on vital rates owing to a lack of basic biological information (Cortes 1999; Beerkircher *et al*. 2003).

Two major demographic models exist – life tables and matrix models. Life tables represent a relatively simple method of laying out a population's reproductive and mortality schedule in a way that will assist in solving a range of biological questions. However, their simplicity has been considered a drawback, whereas elasticity analyses (Simpfendorfer 2004*a*) and elements of stochasticity (Cortes 1999) can be included in matrix models. As a result, matrix models have become increasingly popular in recent years with a strong trend towards their use in fisheries and ecological studies (Simpfendorfer 2004*a*).

The main parameter estimated by demographic analysis is the population's intrinsic rate of natural increase, denoted r (Simpfendorfer 2004*a*). This parameter is a statistical measure of the maximal rate of population growth under optimal conditions assuming a stable age distribution and with constant rates of age-specific mortality and fertility (Krebs 1985; Simpfendorfer 2004*a*). The utility of this value is that a range of scenarios can be modelled using varying input parameters to simulate the population's response to exogenous pressures, such as fishing mortality, and provide insights into the appropriate management or conservation strategies required.

Most demographic studies undertaken have focussed on exploited species in an attempt to determine their respective vulnerabilities and to propose management strategies. Of 64 studies reviewed by Cortes (2004), 58 (90.6%) fell into this category. Although elasmobranchs as a group are considered vulnerable to overfishing (Castro *et al*. 1999), demographic analyses have shown that they encompass a wide continuum of risk. For example, the relatively fast-growing Australian sharpnose shark *Rhizoprionodon taylori* is capable of being sustainably exploited (Simpfendorfer 1999), whereas the lemon *Negaprion brevirostris* and sandbar *Carcharhinus plumbeus* sharks are very vulnerable to exploitation (Cortes 1998).

The Port Jackson shark *Heterodontus portusjacksoni* is a medium-sized, coastal shark endemic to the coastal waters of southern Australia (Last and Stevens 1994). During the austral winter–spring season adults move onto shallow rocky reefs along the east coast of New South Wales to mate and oviposit before migrating, possibly as far south as Bass Strait and the Tasmanian coast (McLaughlin and O'Gower 1971). It is likely that *H. portusjacksoni* is distributed as separate stocks throughout their range, with the east coast population distinct from

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those in southern and western Australia (O'Gower and Nash 1978).

Despite having a basic knowledge of their general biology, there is a distinct lack of vital rate information for *H. portusjacksoni* and heterodontids in general. Data on mortality rates, natural growth rates and growth parameters do not exist, and variations owing to sex or ontogenetic factors are not known for the east coast population. However, this information is vital to the formulation of conservation and management strategies, especially under fishery pressure (Cortes 1998). Although only small-scale commercial and recreational use is currently made of *H. portusjacksoni* (Last and Stevens 1994; Shark Advisory Group 2004) the potential exists for increased use in the future. Hence, rigorous demographic data and analyses are required on the current virgin population, which would also represent the first such approach for any heterodontid species.

The aims of the present study were to determine natural mortality, growth rates and von Bertalanffy growth parameters for embryonic, juvenile, subadult and adult *H. portusjacksoni*; and to conduct demographic analyses to determine the species' population status and to elucidate the maturity stages that are more sensitive to perturbation given their significance as a by-catch species (T. I. Walker, pers. comm.).

Materials and methods

Study species

Adult male and female *Heterodontus portusjacksoni* move onto shallow coastal reefs during the austral winter and spring (June to November on the east coast; hereafter called 'the season') to reproduce (McLaughlin and O'Gower 1971). An oviparous species, females oviposit ~16 egg capsules each year in rocky crevices on these reefs (Powter and Gladstone in press), which take 9–12 months to hatch (Rodda 2000). At eclosion, neonate sex ratios are 1:1 (Powter and Gladstone in press).

On the basis of the development of reproductive organs and habitats occupied, *H. portusjacksoni* was classified into four maturity stages (Powter and Gladstone in press, 2008*a*). Embryonic *H. portusjacksoni* are contained within an egg capsule and are dependent on the yolk sac for nutrition. Juveniles are sexually immature and generally found only in the nursery area; males are <500 mm total length (L_T) and females <600 mm L_T. Subadults are maturing sexually and are not found in nursery areas or adult breeding reefs; males range from 500 mm to <700 mm L_T and females from 600 mm to <900 mm L_T. Adults are sexually mature and generally occur on the breeding reefs during the austral winter and spring; males are ≥700 mm L_T and females ≥900 mm L_T.

Study sites

Adult *H. portusjacksoni* were studied at three shallow (<13 m deep) coastal rocky reefs at Terrigal Haven (33.45°S, 151.45°E), Cabbage Tree Harbour (33.28°S, 151.57°E), and Dent Rock, Jervis Bay (35.07°S, 150.68°E) in New South Wales (NSW), Australia (Fig. 1). Juvenile *H. portusjacksoni* were studied in a shallow seagrass nursery area at Murrays Sandline, Jervis Bay (35.13°S, 150.77°E) (Fig. 1). The seagrass bed consisted of two contiguous regions of 750 m, each of which was divided into three equal zones. The eastern region was closest to the bay's entrance and ranged in depth from 4.2 to 11.4 m (east to west), whereas the western region reached a depth of 6 m at its western end.

Visual surveys and tagging

Underwater visual census (UVC) surveys were conducted at Terrigal Haven twice weekly (one during the day and one during the night) during the season ($n = 131$ surveys) and at least monthly outside the season ($n = 45$). Cabbage Tree Harbour was surveyed four times per month (two day and two night) during the season ($n = 57$) and monthly outside the season ($n = 15$). Dent Rock ($n = 29$) and Murrays Sandline ($n = 29$) were surveyed monthly during daylight hours. Surveys commenced at Terrigal Haven in January 2002, at Cabbage Tree Harbour in July 2002 and at Dent Rock and Murrays Sandline in December 2002, and concluded at the four sites in December 2005. All *H. portusjacksoni* encountered during the surveys were, when possible, captured by hand, sexed, measured (total length (L_T) to the nearest 1 mm) and fitted with uniquely numbered Allflex Lazatags (adults) or Hallprint double T-bar anchor tags (juveniles) in the first dorsal fin. Previously tagged sharks were also captured, sexed and re-measured (to the nearest 1 mm).

Owing to the high number of sharks sighted at Dent Rock a visual population survey was conducted over the entire reef, before the site survey and tagging, from August 2003 to October 2005 during the season ($n = 13$). The sex of all adults sighted was recorded and their L_T estimated to the nearest 50 mm. At Murrays Sandline a visual population survey was conducted every 3 months from September 2003 to December 2005 ($n = 10$) over a 1.5-km section of the nursery that extended 750 m west and 350 m east of the 400-m portion covered during the monthly UVC surveys. L_T was visually estimated (to the nearest 50 mm); however, sex could not be determined owing to the sexually immature state of these individuals.

Commercial fishery samples

A total of 156 male and 104 female *H. portusjacksoni* were obtained from July 2004 to March 2005 from a commercial fish trawler operating in the region of Newcastle, NSW (32.52°S, 151.50°E to 32.49°S, 151.58°E). These catches provided the only source of subadult *H. portusjacksoni*, which were not encountered at the juvenile or adult sites. Length, weight and sex data were also obtained from an additional 478 sharks captured in this fishery (Ramos, unpubl. data). Individuals were weighed (wet weight, nearest 1 g), sexed and measured (L_T, nearest 1 mm).

Growth rates

Growth rates were determined from tag–recapture data using two methods: (*1*) the change in L_T (ΔL_T) of recaptured tagged sharks was regressed against days at liberty and the annual growth rate estimated from the resulting regression equation (Duncan and Holland 2006). The significance of the regression was tested using the coefficient of determination (R^2) and ANOVA after ensuring data was parametric and met the test assumptions; (*2*) the GROTAG maximum likelihood techniques (Francis 1988) were also used to estimate growth rates at two user-selected lengths (α and β), which fall within the length

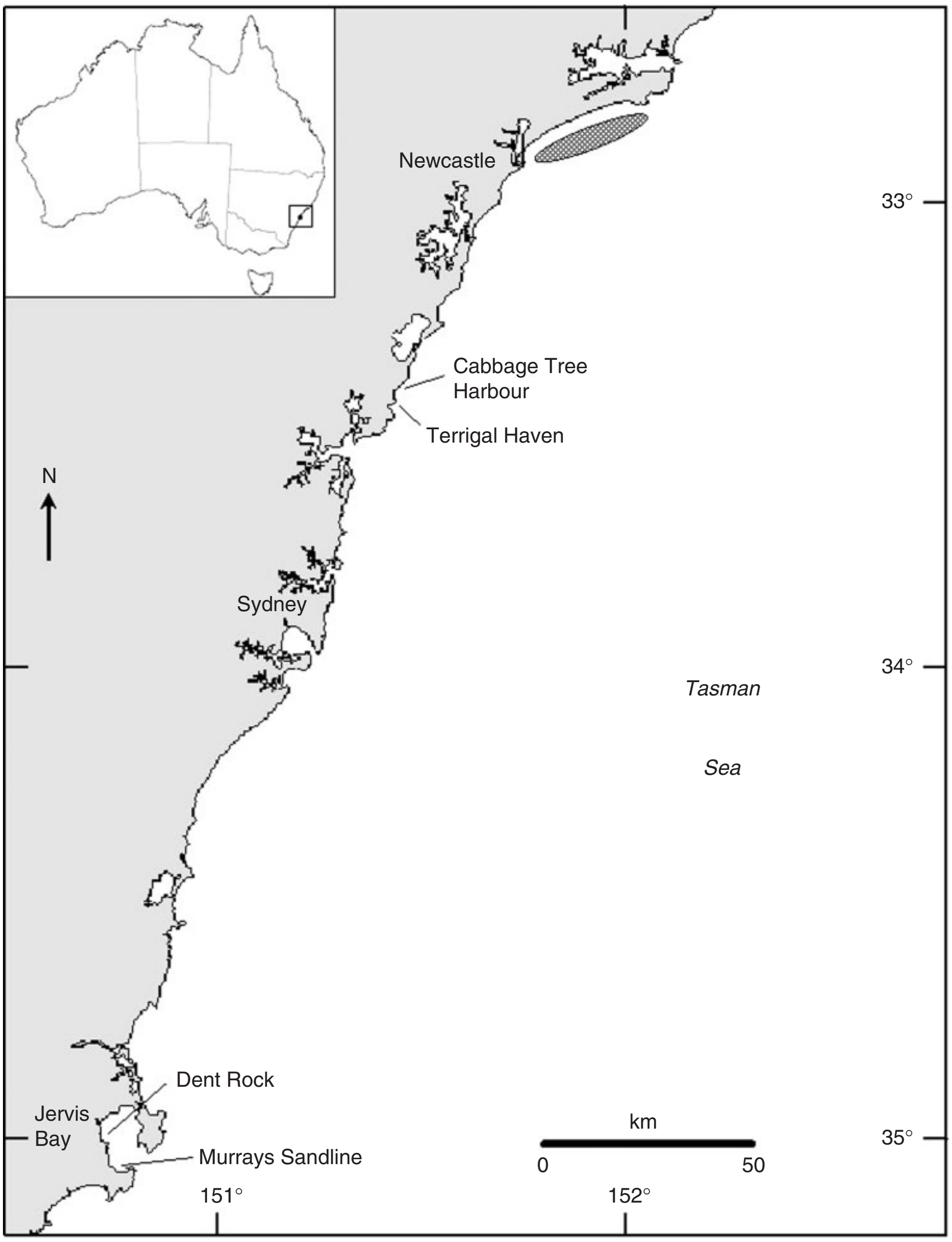

Fig. 1. Map of the central and southern coast of New South Wales, Australia showing the location of the study sites and the area (stippled) from which fishery samples were obtained. Inset map shows the section of the east Australian coast depicted in the main figure.

range of tagged individuals. Modelling commenced with minimal parameters (α and β) and the improvement gained by adding additional parameters determined by log-likelihood ratio (λ) tests. For a significant improvement in fit ($\alpha = 0.05$), the addition of a parameter must increase λ by at least 1.92 (Francis 1988). Modelling was conducted using a Solver-based spreadsheet in Microsoft Excel developed by Simpfendorfer (unpubl. data).

Growth parameters

Growth parameters (K and L_∞), seasonal growth oscillations (C) and growth winter points (WP) were determined for adults and juveniles using growth increment (tag–recapture) analyses within the FiSAT II program (Gayanilo *et al*. 2002). K and L_∞ were also obtained using the Gulland and Holt method as detailed in Sparre and Venema (1998) and Gayanilo *et al*. (2002) along with their associated calculations. Growth parameters for adults were also estimated using the empirical relationships developed by Froese and Binholan (2000) as calculated by the PopDynJFB application (ftp://ftp.cgiar.org/fishbaseftp/PopDynJFB.exe) in Microsoft Excel. The method derives K and L_∞ estimates from given values of maximum length (L_{max}) and length at 50% maturity (L_{50}). L_{max} values were obtained from tagging and fishery data (the present study), whereas L_{50} values were from Powter and Gladstone (in press).

Natural mortality

Natural mortality rates were calculated using one direct and three indirect methods. As *H. portusjacksoni* is not currently subjected to any quantifiable level of fishing mortality, all mortality was assumed to be the result of natural factors, such as senescence and predation (i.e. $F = 0$).

The direct estimate of mortality was obtained using tag-resighting data analysed by Program MARK based on the Cormack–Jolly–Seber (CJS) method. Initially, the fully time-dependent CJS and nested models were run and model suitability assessed on Akaike Information Criterion (AIC) values (Cooch and White 2002). Using bootstrapped goodness-of-fit (GOF) and Program RELEASE GOF (within Program MARK) tests, the model fit and variance inflation factor ($\hat{c}$) were determined. Models with $\hat{c} > 1$ were re-run with a $\hat{c}$-adjustment factor and the best fitting model selected on the basis of corrected AIC (QAICc) values and the normalised Akaike weights (QAICc Weight) as outlined by Cooch and White (2002). Survival rates were estimated from the Program MARK output.

Three indirect estimates of mortality were used to calculate separate mortality rates for juvenile and adult populations. The first indirect mortality estimate used (adults only) was the method of Gunderson and Dygert (1988) which relies on a relationship between female gonadosomatic index (GSI) and natural mortality on the basis that GSI is a proxy for reproductive investment. The Gunderson and Dygert relationship is expressed as $M = 0.03 + 1.68GSI$, where M is the mortality rate and GSI is the gonadosomatic index (Simpfendorfer 2004*b*). Mortality was also estimated using the method of Jensen (1996) which is based on the relationships between life history patterns and natural mortality drawn from the Beverton and Holt life history invariants. Jensen's relationship is expressed as $M = 1.60K$, where M is the mortality rate and K is the von Bertalanffy growth coefficient. The final indirect mortality estimator used was the method of Pauly (1980), which relates natural mortality to von Bertalanffy growth (VBGF) parameters and mean environmental temperature, assuming a relationship between length and natural mortality. The Pauly relationship is expressed as $\log M = -0.0066 - 0.279(\log L_\infty) + 0.6543 (\log K) + 0.4634(\log T)$, where M is the mortality rate, L_∞ is the von Bertalanffy asymptotic length, K is the von Bertalanffy growth coefficient and T is the mean environmental temperature. All VBGF parameters were obtained from growth increment analysis in FiSAT II and the empirical relationships of Froese and Binholan (2000) based on tag–recapture and fishery data, GSI values for adult females at the start of the breeding season (July) were obtained from Powter and Gladstone (in press), whereas mean environmental temperature was calculated using data collected during site and population surveys (Powter 2006).

During site surveys at Terrigal Haven (January 2002 to December 2005) and Dent Rock (July 2003 to December 2005), all egg capsules were examined and mortality calculated (Powter and Gladstone 2008*b*). Embryonic mortality at Terrigal Haven ranged from 0.78 to 0.87 year^{-1} (mean 0.83 year^{-1}) and from 0.87 to 0.90 year^{-1} (mean 0.89 year^{-1}) at Dent Rock.

Table 1. Parameters used to construct 4 × 4 stage-based matrix models using three scenarios across the four life history stages of *Heterodontus portusjacksoni*

A, High mortality, minimum growth and mean fecundity; B, Low mortality, maximum growth and mean fecundity; C, Low mortality, maximum growth and maximum fecundity. Fecundity is the number of female pups per adult female per year; G_i is the probability of an individual surviving and moving to the next stage; P_i is the probability of an individual surviving and remaining in the same stage; and d_j is the stage duration (year) (Simpfendorfer 2004*a*)

Scenario	Parameter	Embryo	Juvenile	Subadult	Adult	Fecundity
A	G_i	0.115	0.001	0.020	–	8
	P_i	–	0.618	0.756	0.888	
	d_j	1	12	10	14	
B	G_i	0.168	0.034	0.109	–	8
	P_i	–	0.741	0.828	0.915	
	d_j	1	8	7	21	
C	G_i	0.168	0.034	0.109	–	10
	P_i	–	0.741	0.828	0.915	
	d_j	1	8	7	21	

Demographic analyses

As age-specific vital rates were not available, demographic analyses were undertaken with a stage-classified matrix model (Caswell 2001) under three different scenarios (Table 1) using the POPTOOLS (v 2.7.1) add-in for Microsoft Excel (http://www.cse.csiro.au/poptools/). For these analyses, individuals were classified into four maturity stages on the basis of morphology and life history characteristics. The models assumed birth pulse; pre-breeding counts; annual reproduction; and, all mature females were reproductively active in a given year. The stage-classified model was constructed after clearly elucidating the life cycle nodes, transition arcs and self-loops and their coefficients. The coefficients were the probability of an individual surviving and moving to the next stage (G_i) or of remaining in the same stage (P_i) and were calculated as described in Simpfendorfer (2004*a*). Stage durations (d_j) were estimated from extrapolations of mean annual growth rates to the maximum size of each maturity stage (the present study), known embryonic period (Rodda 2000) and a longevity estimate of 36 years obtained from three separate indirect methods (Froese and Binholan 2000; Froese and Palomares 2000; Chen and Yuan 2006). Using sectioned vertebrae *H. portusjacksoni* longevity was estimated to be 36 years for males and 44 years for females by Izzo (2005) in South Australia and 24 years for males and 32 years for females by Ramos (2007) in NSW. The matrix models were then used to estimate net reproductive rate (R_o), time to increase the population by a factor of R_o (T), the population growth rate (λ) and the mean generation length (μ_1) (Simpfendorfer 2004*a*).

Elasticities were calculated directly from the matrix model using elements of the transition matrix, the population growth rate (λ) and the elements of the right and left eigenvectors as described in Simpfendorfer (2004*a*). Elasticities identify the stage where a change in vital rates will produce the greatest change in λ (Simpfendorfer 2004*a*). Modified from Mollet and Cailliet (2002), elasticity notations were E_1, E_2, E_3 and E_4 for the fertility, juvenile survival, subadult survival and adult survival elasticities respectively. Elasticity ratios (ER_i) were also calculated ($ER_i \equiv E_i/E_1$) to provide estimates of the scale of exogenous mortality, such as fishing (Mollet and Cailliet 2002). For example, a 10% increase in juvenile mortality would require an [$ER_2 \times 10\%$] increase in fertility to return the population to the pre-disturbance growth rate. The impact of exogenous mortality, such as fishing mortality (F), was assessed by iteratively altering survival rates in particular stages of the matrix and recalculating r (Brewster-Geisz and Miller 2000). The generated values of r were then regressed on F, with the point at which the regression line intersected the x-axis indicating $F_{CRITICAL}$. Values of $F > F_{CRITICAL}$ produce negative r, whereas $F < F_{CRITICAL}$ give positive r values.

Results

Growth rates

A significant linear relationship occurred between ΔL_T and days at liberty for combined sexes and tagging sites in adults ($F_{1,31} = 19.75$, $P < 0.001$). The growth rate (and 95% confidence intervals) estimated from the regression equation was 32.7 mm L_T year^{-1} (15.4–90.7 mm year^{-1}). The regression for adult females from combined sites was significant ($F_{1,23} = 12.23$, $P = 0.002$), but not for males from combined sites ($F_{1,7} = 1.81$, $P = 0.22$) (Fig. 2). The growth rates (and 95% confidence intervals) estimated from the regression equations were 34.3 mm L_T year^{-1} (18.2–101.0 mm year^{-1}) for females from combined sites and 36.4 mm L_T year^{-1} (−13.1–158.5 mm year^{-1}) for males from combined sites, however, the regression for males from combined sites was not significant. A significant linear relationship was found between ΔL_T and days at liberty for adult females at Terrigal Haven ($F_{1,9} = 47.40$, $P < 0.001$), but not for females at Dent Rock ($F_{1,10} = 3.14$, $P = 0.11$) (Fig. 2). The growth rates (and 95% confidence intervals) estimated from the regression equations were 32.7 mm L_T year^{-1} (−11.4–55.9 mm year^{-1}) for females at Terrigal Haven and 39.4 mm L_T year^{-1} (−12.1–133.5 mm year^{-1}) for females at Dent Rock. However, caution must be applied to the Dent Rock estimate owing to the non-significant relationship. Insufficient males were recaptured to conduct regressions for separate sites.

Using the GROTAG method of Francis (1988) the mean annual growth rate for 950 mm L_T (g_{950}) *Heterodontus portusjacksoni* was 31.4 mm, which is similar to the rates estimated through regression of ΔL_T on days at liberty (Table 2). Combining adult and juvenile tag–recapture data produces a range of mean annual growth rates from 64.5 mm (g_{300}) to 10.4 mm (g_{1200}). However, this is in the absence of data relating to individuals in the range 415–875 mm L_T, which may bias the result.

A significant linear relationship was found between ΔL_T and days at liberty for juvenile females ($F_{1,25} = 17.53$, $P < 0.001$), males ($F_{1,12} = 52.23$, $P < 0.001$) and combined sexes ($F_{1,39} = 52.71$, $P < 0.001$) (Fig. 3). The growth rate and 95% confidence intervals estimated from the regression equations were 32.3 mm L_T year^{-1} (12.62–76.75 mm year^{-1}) for combined sexes, 28.2 mm L_T year^{-1} (17.0–73.4 mm year^{-1}) for females and 36.8 mm L_T year^{-1} (9.3–91.3 mm year^{-1}) for males. Using the GROTAG method of Francis (1988) the mean annual growth rate for 270 mm L_T (g_{270}) juvenile

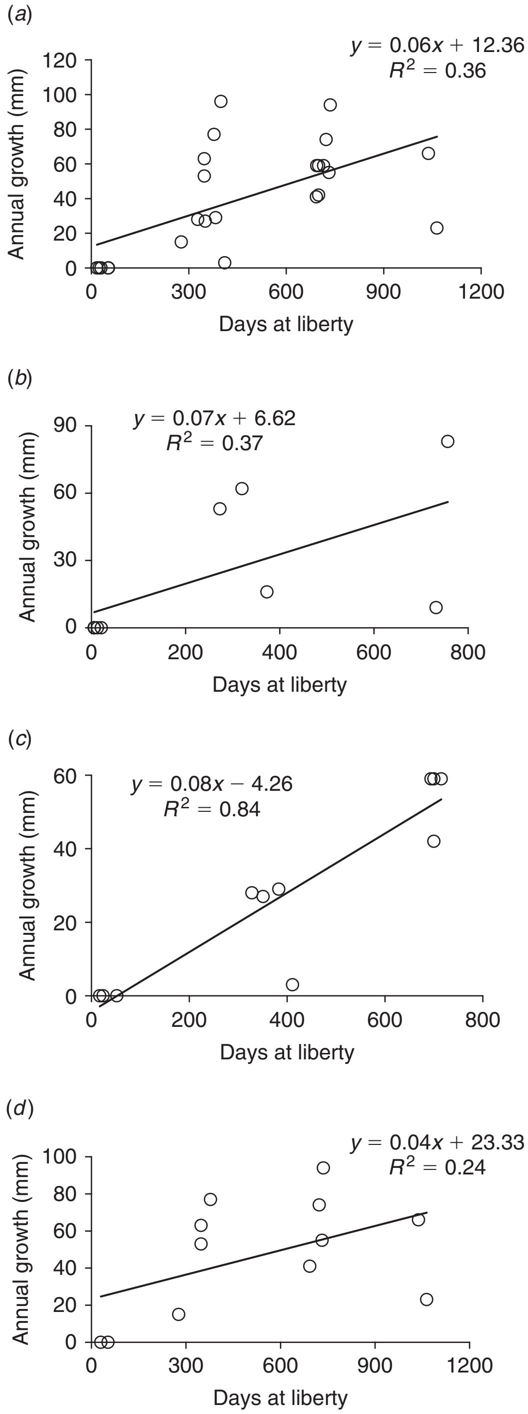

Fig. 2. Regression of annual growth (ΔL_T) against days at liberty for recaptured adult (*a*) female and (*b*) male *Heterodontus portusjacksoni* for all sites combined and for recaptured adult females at (*c*) Terrigal Haven and (*d*) Dent Rock.

H. portusjacksoni was 37.2 mm, which is very similar to the rates estimated through regression of ΔL_T on days at liberty (Table 2). However, the g_{400} growth rate of 17.0 mm L_T year^{-1} is considerably lower than the adult (g_{950}) growth rate of 27.0 mm L_T year^{-1} (Table 2).

Table 2. Log-likelihood functions and parameter estimates of 'best fitting' models for tag–recapture data for adult, juvenile and combined life stages of *Heterodontus portusjacksoni* using the Francis (1988) model

Parameter	Symbol (unit)	Parameter estimates		
		Adult	Juvenile	Combined
Log-likelihood	λ	−121.289	−155.378	−121.289
Reference lengths	α (mm)	950	270	300
	β (mm)	1150	400	1200
Mean growth rates	g_α (mm year^{-1})	31.4	37.2	64.5
	g_β (mm year^{-1})	13.6	17.0	10.4
Growth variability	ν	−0.5	0.0	−0.7
Measurement error	m (mm)	−0.5	10.7	−0.5
	s (mm)	−0.00	2.73	0.00
Outliers	p	0.5	0.0	0.3

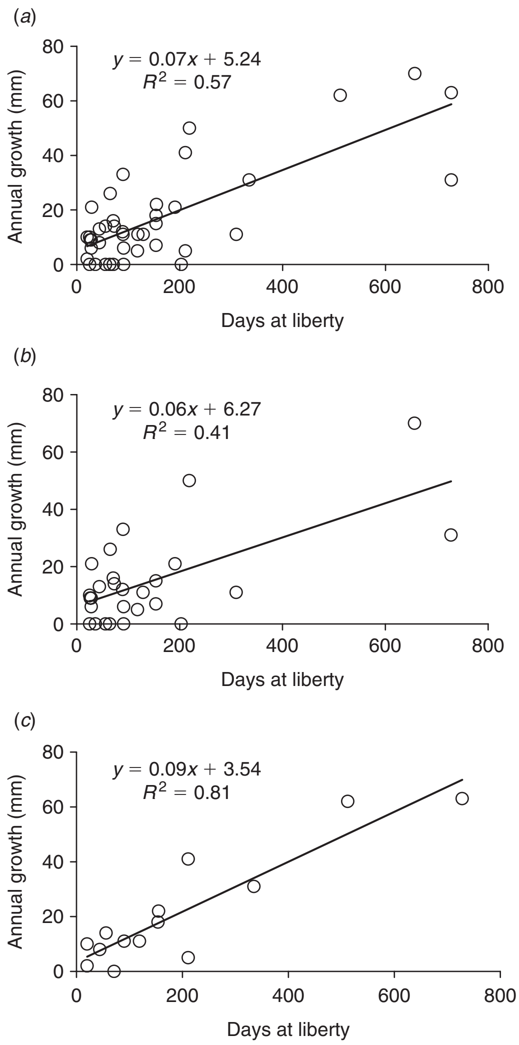

Fig. 3. Regression of annual growth (ΔL_T) against days at liberty for recaptured juvenile *Heterodontus portusjacksoni* at Murrays Sandline for (*a*) sexes combined, (*b*) females and (*c*) males.

Growth parameters

Adult male and female estimates of L_∞ (1261 mm and 1317 mm respectively) and K (0.111 year^{-1} and 0.119 year^{-1} respectively) varied only slightly based on growth increment analysis. Both L_∞ (1374 mm) and K (0.179 year^{-1}) were higher for combined sexes. Seasonal growth oscillations (C) were significant for males, females, and sexes combined. However, male seasonal growth oscillations were large ($C > 1$), whereas that of females and sexes combined were small ($C < 0.2$ and 0.4 respectively). The growth winter point (WP) for males and females was June, with July for combined sexes. Estimates of K obtained from the empirical relationships derived by Froese and Binholan (2000) for adult males and females were lower than those estimated using the Gulland and Holt method (Table 3). L_∞ estimates for females were similar to the Gulland and Holt estimates, however male L_∞ was substantially lower.

Estimates of L_∞ for juvenile males and females (452 mm and 616 mm respectively) and K (0.384 year^{-1} and 0.213 year^{-1} respectively) based on growth increment analysis varied substantially. Both sexes displayed large seasonal growth oscillations, with the value for females ($C < 0.80$) being substantially larger than males ($C < 0.30$). WP was also widely separated (females, July; males, November). The L_∞ (541 mm), K (0.265 year^{-1}), C (<0.60) and WP (July) parameters for the combined sexes were intermediate to males and females considered separately.

Natural mortality

Tag–recapture data for adults at Terrigal Haven and Dent Rock conformed best to the constant survival, time dependent recapture (φ, p_t) model as indicated by the lowest QAICc score (Table 4). The high ΔQAICc score and difference in QAICc weights between models φ, p_t and φ, p provides strong support for the better fit of model φ, p_t to both datasets. Juvenile tag–recapture data conformed best to the constant survival, constant recapture (φ, p) model as indicated by the lowest QAICc score (Table 4). The moderate ΔQAICc score between models φ, p and φ, p_t (Table 4) indicates that there is considerable support for the better fit of model φ, p to the dataset. On the basis of Akaike weights, the model φ, p has 5.43 times the support of the alternate model.

Table 3. Growth parameter (L_∞ and K) estimates derived from maximum length (L_{max}) and length at 50% maturity (L_{50}) for adult female and male *Heterodontus portusjacksoni* using the empirical relationships derived by Froese and Binholan (2000)

L_{50} obtained from Powter and Gladstone (in press)

	Input parameters		L_∞ (mm)	K (year^{-1})
	L_{max} (mm)	L_{50} (mm)		
Female[A]	1309	902	1341	0.08
Female[B]	1218	902	1249	0.09
Female[C]	1264	902	1295	0.09
Male[A]	1076	767	1105	0.09
Male[B]	1029	767	1058	0.09
Male[C]	1053	767	1082	0.09

L_{max} derived from: [A]survey data; [B]fishery sample; [C]combined survey and fishery data.

On the basis of tag–recapture data, mortality (and 95% confidence limits) was estimated to be 0.063 $year^{-1}$ (0.007–0.378 $year^{-1}$) for adults at Terrigal Haven and 0.074 $year^{-1}$ (0.040–0.132 $year^{-1}$) for adults at Dent Rock. Both male and female mortality estimates based on the method of Jensen (1996) were substantially higher than the other indirect methods (Table 5). The estimates provided by the Pauly (1980) method were closer to those obtained from tag–recapture analysis, but still considerably higher, whereas those obtained via the Gunderson and Dygert (1998) method were approximately twice as high as tag–recapture rates.

Juvenile mortality (and 95% confidence limits) at Murrays Sandline was estimated at 0.225 $year^{-1}$ (0.165–0.299 $year^{-1}$) on the basis of tag–recapture analysis. The indirect mortality estimates from the Pauly (1980) method were relatively consistent with the tag–recapture mortality estimates, although males were higher (Table 5). As with adults, the mortality estimates obtained using the Jensen (1996) method were substantially higher than the Pauly (1980) and tag–recapture mortality rates.

Demographic modelling

Regardless of the scenario adopted, *H. portusjacksoni* has very low intrinsic rates of increase (r) and finite rates of population increase (λ) (Table 6). Scenario A involved the use of 'worst case' parameters (Table 1) which resulted in a negative r value and a negligible net reproductive rate (R_o), indicative of a declining population. Scenarios B and C resulted in annual population growth estimates of 1.0% and 2.4% respectively. The net reproductive rates of these models were similar (Table 6), as was the time required to increase the population by a factor of R_o (T) and the mean generation length (μ_1). The elasticity ratio (ER) scores in all three models reveal that changes in survival at the adult stage would have the greatest impact on population growth (Table 6). In scenarios B and C, the adult stage has approximately twice the impact on population growth as subadults and approaching three times the impact of juveniles.

The stable stage structure values from the matrix reveal decreasing contributions as maturity increases with subadults and adults each representing 5.7% of the population compared with 33% for juveniles and 55.6% for embryos. However, the reproductive contribution by adults (61.2%) accounts for almost two-thirds of the total, with much lower values for subadults (34.1%), juveniles (4.1%) and embryos (0.7%).

Factoring additional adult mortality into the stage-classified matrix model to simulate fishing or other exogenous mortality factors shows a linear relationship between r and increased mortality (Fig. 4). Using this relationship, it can be determined that an increase in adult stage mortality of 0.07 will reduce r to zero, whereas an increase greater than 0.07 will generate negative r values.

Discussion

Growth rates

Adult and juvenile *Heterodontus portusjacksoni* exhibited very slow rates of growth compared with other elasmobranchs (Branstetter 1990; Avsar 2001; Barker *et al*. 2005). Regression methods provided a combined sex estimate for adults of 32.7 mm $year^{-1}$, which is quite similar to the 31.4 mm $year^{-1}$ (g_{950}) estimated by the Francis (1988) GROTAG model. Significantly, the combined sex growth rates for adults and juveniles were quite similar. The regression estimate of 32.7 mm $year^{-1}$ for adults was very similar to the 32.3 mm $year^{-1}$ for juveniles. However, the GROTAG estimates for juveniles ($g_{270} = 37.5$ mm $year^{-1}$) were slightly higher than adults ($g_{950} = 31.4$ mm $year^{-1}$). Typically adult growth rates in elasmobranchs are appreciably less than those of juveniles (Cortes 2000*a*). However, the departure from this pattern in

Table 4. Corrected Akaike Information Criterion (QAICc) values, model deviance and likelihood scores for the fully time-dependent Cormack–Jolly–Seber model (φ_t, p_t) and nested models based on tag–recapture data with corrections for the calculated variation factor ($\hat{c}$)

Upper panel for adults at Terrigal Haven from 2002 to 2005 ($\hat{c} = 1.39$); middle panel for adults at Dent Rock from 2003 to 2005 ($\hat{c} = 1.292$); lower panel for juveniles at Murrays Sandline from 2002 to 2005 ($\hat{c} = 1.04$)

Model	QAICc	ΔQAICc	QAICc weight	Likelihood	Parameters	Deviance
Adults – Terrigal Haven						
φ, p_t	170.02	0.00	0.992	1.000	13	61.85
φ, p	179.60	9.58	0.008	0.008	2	97.01
φ_t, p	191.67	21.65	0.000	0.000	13	83.50
φ_t, p_t	197.91	27.89	0.000	0.000	23	61.02
Adults – Dent Rock						
φ, p_t	293.31	0.00	0.975	1.000	16	152.20
φ, p	300.64	7.33	0.025	0.026	2	192.71
φ_t, p	322.32	29.00	0.000	0.000	16	181.20
φ_t, p_t	326.74	33.43	0.000	0.000	29	145.58
Juveniles – Murrays Sandline						
φ, p_t	556.46	3.38	0.156	0.184	28	156.56
φ, p	553.07	0.00	0.844	1.000	2	209.87
φ_t, p	573.21	20.14	0.000	0.000	28	173.32
φ_t, p_t	596.16	43.08	0.000	0.000	51	138.46

Table 5. Indirect mortality estimates for (upper panel) adult and (lower panel) juvenile *Heterodontus portusjacksoni*
Source model indicates the model used to calculate von Bertalanffy growth (VBGF) parameters

Mortality estimate method	Sex	Source model	Data inputs *GSI*	L_∞ (mm)	*K* (year^{-1})	Temp (°C)	*M* (year^{-1})
Adults							
Gunderson and Dygert	Female		0.005				0.120
Jensen	Combined	Gulland and Holt			0.179		0.286
	Female	Gulland and Holt			0.119		0.190
	Female	Froese and Binholan[A]			0.08		0.128
	Female	Froese and Binholan[B,C]			0.09		0.144
	Male	Gulland and Holt			0.111		0.178
	Male	Froese and Binholan[A,B,C]			0.09		0.144
Pauly	Combined	Gulland and Holt		1374	0.179	16.6	0.157
	Female	Gulland and Holt		1317	0.119	16.6	0.121
	Female	Froese and Binholan[A]		1341	0.08	16.6	0.093
	Female	Froese and Binholan[B]		1247	0.09	16.6	0.103
	Female	Froese and Binholan[C]		1295	0.09	16.6	0.102
	Male	Gulland and Holt		1261	0.111	16.6	0.117
	Male	Froese and Binholan[A]		1105	0.09	16.6	0.106
	Male	Froese and Binholan[B]		1058	0.09	16.6	0.107
	Male	Froese and Binholan[C]		1052	0.09	16.6	0.107
Juveniles							
Jensen	Combined	Gulland and Holt			0.265		0.424
	Female	Gulland and Holt			0.213		0.341
	Male	Gulland and Holt			0.384		0.641
Pauly	Combined	Gulland and Holt		541	0.265	18.5	0.276
	Female	Gulland and Holt		616	0.213	18.5	0.231
	Male	Gulland and Holt		452	0.384	18.5	0.370

[A]Tag–recapture data; [B]fishery data; [C]combined data.

Table 6. Summary of demographic results for *Heterodontus portusjacksoni* using 4 × 4 stage-based matrix models on three scenarios
A, High mortality, minimum growth and mean fecundity; B, Low mortality, maximum growth and mean fecundity; C, Low mortality, maximum growth and maximum fecundity. E and ER values calculated as in Mollet and Cailliet (2002); scenario values are set out in Table 1

Scenario	A	B	C
Stage duration[A] (year)	1–12–10–14	1–8–7–21	1–8–7–21
λ	0.89	1.01	1.024
r (year^{-1})	−0.118	0.013	0.024
R_o	0.002	1.312	1.640
T (year)	52.33	21.53	20.77
μ_1 (year)	16.62	22.50	22.50
E_1	0.0008	0.049	0.052
E_2 (ER_2)	0.002 (3.29)	0.181 (3.73)	0.188 (3.62)
E_3 (ER_3)	0.005 (6.70)	0.266 (5.48)	0.271 (5.22)
E_4 (ER_4)	0.992 (1318.8)	0.505 (10.41)	0.489 (9.43)

[A]Stage duration in years for embryo–juvenile–subadult–adult.

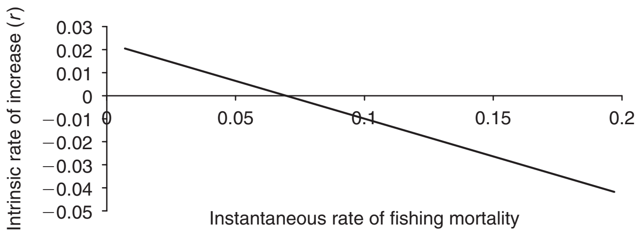

Fig. 4. Relationship between the intrinsic rate of increase (*r*) and simulated fishing mortality (*F*) on the adult stage using stage-classified Model C (low mortality, maximum growth and maximum fecundity).

H. portusjacksoni may indicate that the life history strategy of rapid juvenile growth to offset predation (Branstetter 1990) may not apply in this species.

Growth rates in juvenile elasmobranchs are often considered in terms of the life history strategy adopted to avoid predation owing to small size (Branstetter 1990). Generally, slow-growing species are born at large size or use protected nursery grounds, whereas the faster-growing species rely on rapid growth to maximise survival. *H. portusjacksoni* juveniles fall into the first group, with their birth length ~19% of L_∞ and their juvenile stage spent in seagrass bed nursery areas that afford them protection via disruptive colouration (Powter and Gladstone 2008*a*). This is further supported by the mortality rate of juveniles in the present study being lower than many other elasmobranchs (Manire and Gruber 1993; Heupel and Simpfendorfer 2002).

However, their sharp dorsal spines may also serve to reduce predation. Strong (1989) found juvenile *Heterodontus francisci* were either regurgitated uninjured or avoided by angel sharks *Squatina californica*. Although predatory attacks were not observed on any juveniles during the present study, several observations suggest juvenile *H. portusjacksoni* gain similar advantage from their dorsal spines. Despite examining over 400 individual juveniles, only three (0.8%) were observed with injuries consistent with apparent predation attempts. All three appeared healthy and with fully healed wounds that resembled crescent-shaped bite marks on their flanks as if bitten from above the first dorsal fin while resting on the substrate. It is probable that an attack of this type brought the very sharp dorsal spines into contact with the predator's mouth and resulted in the juvenile being released. Hence juvenile *H. portusjacksoni* appear to have an early life history stage that minimises predation without requiring rapid growth.

Juvenile male *H. portusjacksoni* growth rates (36.8 mm year^{-1}) were markedly higher than females (28.2 mm year^{-1}). However, both growth rates were still comparatively slow. Branstetter (1990) found the growth rates in the first year of several carcharhinid and lamnid sharks ranged from 16% of birth length (BL) (*Carcharhinus obscurus*) to 100% BL (*Galeocerdo cuvier*). In neonate *H. portusjacksoni*, the annual growth rate of 37.2 mm L_T represents ~14.5% to 16.8% BL, placing them at the bottom of the group examined by Branstetter (1990).

McLaughlin and O'Gower (1971) estimated the annual growth rate of juvenile *H. portusjacksoni* at 50–60 mm based on four captive neonates that survived for between 420 and 780 days. This rate is significantly faster than the 36.8–37.5 mm determined in the present study on the basis of 41 recaptured individuals at liberty for up to 728 days after tagging. However, growth rates in some elasmobranchs have been shown to be faster in captivity than the wild (Branstetter 1987; Carrier and Luer 1990). It is likely that the rates observed by McLaughlin and O'Gower (1971) reflected more rapid growth rates in captivity, the inaccuracy of a small sample or both, whereas the rates determined in the present study more accurately reflect the growth rate of wild juvenile *H. portusjacksoni*.

Based on regression analyses, the growth rates of adult males (36.4 mm year^{-1}) were marginally faster than those of adult females (34.3 mm year^{-1}), which is typical of many sharks (Carlson and Parsons 1997). The growth rates determined for adult *H. portusjacksoni* in the present study are similar to those estimated for captive adults by McLaughlin and O'Gower (1971). Based on five captive adults that survived for over one year, they estimated annual growth to be between 20 and 40 mm. Similarly, a single female crested horn shark, *Heterodontus galeatus*, hatched in captivity had a mean annual growth rate of 32 mm between the ages of 7 and 12 years (Whitley 1950). Tovar-Avila (2006) reported annual growth rates of 8.4 mm year^{-1} for captive *H. portusjacksoni* and 46.8 mm year^{-1} for tagged–recaptured sharks in the wild from far eastern Victoria. However, this was based on only five and seven individuals, respectively, and across lengths spanning several maturity stages.

Growth parameters

Although the growth rates of adult male and female *H. portusjacksoni* were different, the K values were quite similar, with little variation in their values regardless of the method used. Asymptotic length (L_∞) estimates derived from the empirical relationships of Froese and Binholan (2000) more closely matched known total lengths (Powter 2006) and published reports (Last and Stevens 1994; Compagno 2002) than those using Gulland and Holt. The Froese and Binholan estimates of L_∞ and K also produced mortality estimates that closely matched those obtained from tag–recapture analyses when factored into the Pauly (1980) equation. Hence, the Froese and Binholan generated L_∞ and K estimates appear to be the more appropriate for *H. portusjacksoni*.

Growth coefficient estimates for juveniles were much higher than adults and substantially different between the sexes, with female juvenile *H. portusjacksoni* having lower K values (Table 2). K estimates from the GROTAG model were significantly lower for combined sexes; however, the failure to account for seasonal growth oscillations may have contributed to this difference. These growth oscillations were significant in both sexes, but stronger in female juveniles ($C < 0.80$) than males ($C < 0.30$). Although the models predicted winter points for females in July and males in November, analysis of tag–recapture data shows a distinct pattern of reduced, or absent, growth during the winter months followed by more rapid growth outside this season (Powter 2006). These growth oscillations are clearly temperature-related, with mean water temperatures at Murrays Sandline falling to 16.1°C (±0.40°) in winter and 17.0°C (±0.52°) in spring before rising to 19.9°C (±0.38°) in autumn and 20.3°C (±0.64°) in summer (Powter 2006). Despite this, the GROTAG estimate of $K = 0.169$ year^{-1} is more consistent with the slow observed growth rate for juvenile *H. portusjacksoni* and with the comparative growth rates and K values for adults.

Using stochastic VBGM methods to estimate growth parameters for *H. portusjacksoni* based on parameterisation of growth heterogeneity on length-at-age data, Tovar-Avila (2006) reported more rapid growth during the early years of life than after maturity. Although not quantifying individual parameters for different maturity stages, the K values of 0.07 year^{-1} for females and 0.084 year^{-1} for males were lower than the present study, but L_∞ values were similar. The variation in growth rates and parameters between the two studies may be attributable to the use of indirect, model-based estimates by Tovar-Avila (2006) compared with the direct tag–recapture-based methods of the present study.

Natural mortality

Mortality rates for adult *H. portusjacksoni* were substantially lower using tag–recapture data than any of the indirect methods used. The methods of Gunderson and Dygert (1988) and Jensen (1996) estimated mortality to be approximately two to four times higher than rates derived from tag–recapture data. The Pauly (1980) method gave much closer mortality estimates, especially if the input parameters were those derived from the Froese and Binholan (2000) relationships. It is worth noting that the Pauly (1980) method is affected by the mean water temperature in which the individual lives. The calculations in the present study were based on a mean water temperature of 16.6°C, which was derived from the water temperatures measured at Terrigal Haven and Dent Rock during the onshore reproductive season

(Powter 2006). It is likely, however, that the mean water temperature in which adult *H. portusjacksoni* occurs throughout their entire life cycle is lower than 16.6°C, given their likely southerly and/or offshore migrations (Powter 2006). Any reduction in the mean water temperature value would lead to a reduction in the mortality rate derived from the Pauly (1980) method. However, all indirect mortality estimates may be susceptible to major bias when estimating natural mortality.

The low natural mortality rates found for adult *H. portusjacksoni* (0.063–0.074 year^{-1}) are consistent with the generally low mortality of most elasmobranchs (Stevens *et al*. 2000). The natural mortality rate of piked spurdog *Squalus megalops* was estimated at 0.085 year^{-1} (Braccini 2006); the spiny dogfish *Squalus acanthias* at 0.092 year^{-1} (Rago *et al*. 1998) and the finetooth shark *Carcharhinus isodon* at 0.067–0.071 year^{-1} (Carlson *et al*. 2003). However, mortality estimates for *H. portusjacksoni* in far eastern Victoria ranged from 0.11 to 0.13 year^{-1} (Tovar-Avila 2006), but were based on indirect methods which may be susceptible to bias.

The comparative values of the mortality estimates for juvenile *H. portusjacksoni* follow a similar pattern to that of the adults, with the Jensen (1996) estimates being ~1.5 to 3.0 times higher than the tag–recapture-derived values. As with adults, the Pauly (1980) mortality estimates are similar, albeit marginally higher, than tag–recapture mortality rates. Nonetheless the tag–recapture-based estimate of mortality for juvenile *H. portusjacksoni* (0.225 year^{-1}) is lower than that of other juvenile sharks (Manire and Gruber 1993; Heupel and Simpfendorfer 2002). It is possible that the juvenile mortality is even lower owing to the effect of emigration; however, the site fidelity exhibited by juvenile *H. portusjacksoni* would decrease the magnitude of this effect (Powter 2006). The best estimates of natural mortality in both adult and juvenile *H. portusjacksoni* come from tag–recapture analyses.

Demographic analyses

Demographic analyses of *H. portusjacksoni* show that the species has low values of r, λ and R_o, with correspondingly high values of T and μ_1. Although R_o and T are often used to describe generation times, Mollet and Cailliet (2002) caution against their use in matrix models with few stages. Instead, they consider μ_1 a better estimate of generation time, which suggests that the mean length of a generation in *H. portusjacksoni* is 22.5 years. At values of $r = 0.069$ year^{-1} for adults and $r = 0.225$ year^{-1} for juveniles, *H. portusjacksoni* has a low intrinsic rate of increase in comparison to other elasmobranch species (Branstetter 1990; Campana *et al*. 1999; Bishop *et al*. 2006). Combined with this, the low mortality, slow growth rate, low K, late maturity and likely high longevity places *H. portusjacksoni* within the elasmobranch group generally considered as K-selected (Krebs 1985; Frisk *et al*. 2001).

Examining the conservation of long-lived marine animals, Musick (1999) considered that species with $K \leq 0.1$ year^{-1} or $r < 0.1$ year^{-1} are particularly vulnerable to collapse if subjected to additional mortality and that recovery could take decades. Adopting a similar approach, Frisk *et al*. (2001) found elasmobranchs fell into three size groups that generally reflected their life histories and susceptibility to collapse. They found species of medium to large size ($L_{max} = 100$–199 cm L_T) were particularly susceptible to collapse when exploited and generally had a reduced ability to rebound from population depletion. Investigating rebound potentials, Smith *et al*. (1998) also found coastal species that were medium to large-size, slow-growing and late to mature had the lowest recovery capabilities. These sharks, which included leopard (*Triakis semifasciata*), dusky (*Carcharhinus obscurus*), bull (*Carcharhinus leucas*), sandbar (*Carcharhinus plumbeus*), seven gill (*Notorynchus cepedianus*) and lemon sharks (*Negaprion brevirostris*) appeared to be selected for a long reproductive life. On the basis of L_{max}, K and r, *H. portusjacksoni* falls into this group of susceptible species.

The current fishery practices impacting *H. portusjacksoni* in far eastern Victoria represent a low risk (Tovar-Avila 2006). However, retention for market as a by-product or increased post-capture mortality would increase this to medium and potentially have major effects on the population's viability. In this population, analyses considered juvenile survival to have the largest impact on population growth; however, these did not take account of the very high natural levels of embryonic mortality (Powter and Gladstone 2008*b*) used in the present study. As such, the long-term reproductive potential of adult females may have been underestimated.

An increase in mortality across all stages equivalent to r will reduce population growth to zero (Mollet and Cailliet 2002). On this basis a mortality increase of 0.013 to 0.0124 year^{-1} across all stages will lead to zero population growth. However, the matrix elasticities and elasticity ratios indicate that the adult population is the stage that has the greatest impact on the rate of population growth. In fact, the elasticity ratios show that changes in the adult population survival will have twice the effect of changes in the subadult stage and three times that of the juvenile stage. The scale of the impact is also quite significant. Impacts leading to a 10% decrease in adult survival would require a 94.3% to 104.1% increase in fertility to return the population to the same growth rate as the current virgin population.

A potential source of exogenous mortality for *H. portusjacksoni* comes from the development of a commercial fishery. Currently a small market exists within the Southern and Eastern Scalefish and Shark Fishery (SESSF), with *H. portusjacksoni* having the ninth highest catch rate of all sharks in the fishery, and with recreational anglers (Last and Stevens 1994; Shark Advisory Group 2004; T. I. Walker, pers. comm.). Significant by-catch also occurs in many fisheries throughout their range; however, separate catch statistics are generally not kept for *H. portusjacksoni*, which is classified within the group 'other shark'. A recent fishery-independent assessment of the NSW Ocean Trawl Fishery found that the frequency of occurrence of *H. portusjacksoni* in sample trawls on the shelf ranged from 20.1% to 64.1% of the non-commercial species catch (NSW Department of Primary Industries 2004), whereas *H. portusjacksoni* is the second most important by-catch species, after *Cephaloscyllium laticeps*, in the shark fishery of southern Australia with ~6000 animals per year caught and discarded (T. I. Walker, pers. comm.). Hence, little or no additional fishing effort would be required to exploit this resource.

Factoring additional mortality on the adult stage into the stage-based matrix model indicates that fishing mortality (F) of 0.07 year^{-1} would reduce population growth (λ) to zero, whereas

$F > 0.07$ year^{-1} would generate negative values of r. Thus, a relatively low level of total mortality (Z) exceeding 0.133 year^{-1} at the adult stage would see a decline in the population. However, this must be considered in light of the inability of typical demographic models to account for density-dependent variation in life history parameters (Au and Smith 1997). As a result the fishery impacts on a population may be overestimated by demographic models.

Nonetheless, the combination of medium-large size, slow growth rate and late maturation of *H. portusjacksoni* make them susceptible to suffering significant population declines should they be exploited, even at the low level outlined above. Furthermore, the lengthy mean generation time ($\mu_1 = 22.5$ year) means any such declines would be likely to take many years to become apparent. Equilibrium strategist elasmobranchs, like *H. portusjacksoni*, represent the species that are least resilient to fishing (Smith *et al*. 1998). Hence protection of the reproductive stock is a priority as all of the years during which each female is reproductively active are likely to be necessary to simply ensure that at least one pup of each sex survives to adulthood.

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