Comparative rates of growth of the Port Jackson shark throughout its southern Australian range

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Abstract. Port Jackson sharks are distributed throughout southern Australia, with evidence suggesting that potential subpopulations exist. If subpopulations are evident, then phenotypic variation among groups should result in differences in life-history parameters. The present study tested for patterns of spatial variability of life-history parameters among regional Port Jackson shark populations. Rates of growth from Port Jackson sharks caught in the gulf waters of South Australia were calculated on the basis of counts of vertebral increments. Growth parameters were obtained by fitting the length-at-age data to von Bertalanffy and Gompertz growth functions. While the derived growth curves fit the length-at-age data well ($r^2$ ranged from 0.87 to 0.91), parameters showed considerable differences between the two functions, with the von Bertalanffy function providing the more realistic estimates of growth (combined sexes: $k = 0.081$ year$^{-1}$, $L_{\infty} = 1232$ mm total length and $t_0 = -1.937$ years). Life-history parameters for South Australian Port Jackson sharks were collated with the available data for the species, facilitating comparisons among regional populations. Growth curves among populations varied significantly; however, considerable overlap in the length ranges of size at birth and sizes at maturity among populations were evident. Overall, the data presented here do not provide definitive support for the presence of subpopulations across the distribution of the Port Jackson shark, suggesting that molecular analysis maybe required to directly test for structuring.


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Introduction

The identification and delineation of subpopulations within the distribution of species of fish (i.e. teleosts and elasmobranchs) is fundamental in fisheries science, providing the spatial framework for appropriate management and conservation strategies to maintain fish resources as well as preserving genetic diversity (Begg and Waldman 1999; Booke 1999; Abaunza 2008). Yet for elasmobranchs (sharks, rays and skates), few species have been examined for population structure via genetic analysis (Heist 2004; Daly-Engel et al. 2010), and limited focus has been given to utilising the elemental composition of the calcified tissues of elasmobranchs for testing patterns of structuring (Edmonds et al. 1996; C. Izzo and B. M. Gillanders, unpubl. data).

Subpopulations of a species of fish are generally considered to be spatially and/or temporally isolated groups (Hissen et al. 1981; Begg et al. 1999a). The accumulation of genotypic and/or environmental factors results in the phenotypic variation of intrinsic life-history parameters among isolated groups, e.g. growth, recruitment, and natural and fishing mortality (Begg et al. 1999b). For elasmobranchs, spatial differences in one or more life-history parameter provide a common means for investigating population structuring, because of the relative ease of obtaining estimates of these parameters (Begg et al. 1999b; Pawson and Ellis 2005). Several species of elasmobranchs have been shown to display latitudinal and/or geographic differences in rates of reproduction and growth (e.g. Parsons 1993; Lombardi-Carlson et al. 2003; Farrell et al. 2010).

Yet, for many species of elasmobranchs, little is known about their life histories (Cailliet and Goldman 2004), impeding species-specific assessments of exploitation susceptibility and appropriate management action (Frisk et al. 2001). This is particularly problematic for elasmobranchs because they are characterised as possessing life histories that render them susceptible to fishing pressure, i.e. slow growth to large sizes, compounded by protracted maturity and low fecundities (Hoening and Gruber 1990; Walker 1998; Stevens et al. 2000).

The Port Jackson shark (\textit{Heterodontus portusjacksoni} Meyer, 1793) is a demersal elasmobranch species endemic to continental shelf waters of southern Australian (Last and Stevens 2009). The Port Jackson shark is commonly caught as by-catch by commercial and recreational fishers throughout the species distribution range (Walker et al. 2005; Jones et al. 2010),
and accordingly, has received interest from fishery scientists, as assessments of the population demography of the Port Jackson shark have been made for south-eastern Australian populations (Powter and Gladstone 2008a; Tovar-Avila et al. 2010). However, no assessment has been made of the population age structure of the Port Jackson shark for South Australia, the approximate centre of the species distribution.

Several lines of evidence, including the tagging and recapture of individuals (McLaughlin and O’Gower 1971; Powter 2007; Rodda and Svane 2007a), the strong natal home-site fidelity (philopatry) of the species (O’Gower 1995; Powter and Gladstone 2009), as well as the analysis of allozyme-loci variation (O’Gower and Nash 1978) and vertebral elemental composition (C. Izzo and B. M. Gillanders, unpubl. data), suggest that within the range of the Port Jackson shark, there may exist multiple, broadly distributed subpopulations.

On the basis of allozymic variation, O’Gower and Nash (1978) suggested that two subpopulations of Port Jackson sharks occupy different biogeographic regions, namely, a south-western population from Western Australia to northern Victoria and a north-eastern population off New South Wales that includes southern Queensland (Fig. 1). The presence of the proposed subpopulations of Port Jackson sharks concurs with the general eastern and western biogeographic regions delimited by the Bassian Isthmus (Fraser et al. 2009). Yet, O’Gower and Nash (1978) indicated that finer, localised groupings within these biogeographic regions may be evident.

Given the evidence presented here, it is expected that phenotypic variation among regional populations of Port Jackson sharks should result in significant differences among life-history parameters (e.g. rates of growth and reproduction). These differences may be considered further evidence for population structuring of the Port Jackson shark and may be used to better define the spatial extent of regional subpopulations.

![Approximate distributions of the two biogeographic regions for the Port Jackson shark as suggested by O’Gower and Nash (1978).](image)

The present study provides the first growth estimates for the South Australian Port Jackson shark, based on the count of vertebral growth increments. The findings generated here will be collated with the available demographic data to test for the presence of subgroups by identifying patterns of spatial variability of life-history parameters among multiple regional Port Jackson shark populations.

### Materials and methods

#### Sampling

In total, 180 Port Jackson shark specimens (107 females and 73 males) were collected from the Spencer Gulf and Saint Vincent’s Gulf in South Australia between 2003 and 2008, on-board commercial and research trawl-fishing vessels (Fig. 1). On capture, specimen sex was determined on the basis of external morphology, and total body lengths ($L_T$) and bodyweights ($W_B$) were recorded (to the nearest millimetre and gram, respectively). Specimens were then euthanased and sections of vertebrae ($n = 8–12$) were collected from below the first dorsal fin.

#### Vertebral preparation

Estimates of specimen ages were based on counts of growth increments in the vertebral centra. Annual increment periodicity has been partially verified in the vertebrae of the Port Jackson shark (Ramos 2007); however, annual increment formation has been validated for the dorsal fin spines of the species (Tovar-Avila et al. 2008). Given that corresponding sectioned fin spines and sectioned vertebral centra possess equivalent counts of growth increments (Tovar-Avila et al. 2009a), it was assumed that counts of sectioned vertebrae accurately estimated the ages of Port Jackson sharks. Moreover, the vertebral increment pattern provides greater reader confidence than do corresponding counts of growth increments in dorsal fin spines (Tovar-Avila et al. 2009a).

Individual vertebral centra were separated and excess tissue was removed using a scalpel, before soaking the structure in a solution of 3.5% NaCl for 10–20 min, depending on the size of the centra. Vertebral centra were rinsed in fresh water and allowed to air dry. The vertebral centrum diameter ($D_{VC}$) was measured to the nearest millimetre using digital callipers. Two vertebrae from each specimen were embedded in a clear-setting epoxy resin and transverse sections $\sim 300 \mu m$ thick were cut using a lapidary saw. Vertebral sections were then mounted on glass microscope slides for examination.

#### Counts of growth increments

Counts of growth increments were made under a dissecting microscope with a transmitting light source. Vertebral growth increments were defined as a pair of opaque and translucent bands, with each increment representing one growth cycle (Tovar-Avila et al. 2009a). Counts of increments commenced after the birth ring (age = 0), which was identified as a change in the angle of the outer edge of the corpus calcareum. Counts of growth increments were adjusted for the date of capture, assuming a theoretical date of hatching of 29th of January (Rodda and Seymour 2008).
Multiple, non-consecutive counts were made for one vertebra per specimen by a single experienced reader (8+ years experience). Samples were examined without prior knowledge of specimen size, sex or previous increment count. A consensus increment count was reached when two counts from three separate reading periods coincided. A level of reader confidence, ranked on a scale from 1 (unreadable = low reader confidence) to 5 (exceptionally clear increments = high reader confidence), was assigned to each reading on the basis of increment clarity (Officer et al. 1996). The variability and precision of the repeated counts was analysed using the coefficient of variation and index of precision (Chang 1982), as well as the index of average percentage error (IAPE) (Beamish and Fournier 1981).

Analyses of growth

Length-at-age data were fitted to the von Bertalanffy (1938) growth function (VBGF), the most commonly used growth model in fisheries science (Haddon 2001), thus providing growth function (VBGF), the most commonly used growth function. Analyses of growth were made using the FISHPARM software package (Prager et al. 1989). Sex-specific comparisons of growth were made by analysis of covariance (ANCOVA) of the least-squares linear regression of the length-at-age data (Natanson et al. 2002). Residual plots were examined to verify that the error terms satisfied the assumptions of normality and homogeneity of variance. Statistical analyses were performed using SPSS v15.0 (SPSS, Inc., Chicago, IL, USA).

Comparisons among regional populations

Relevant information for the demography and biology of the Port Jackson shark throughout the species distribution was collated from published papers and unpublished theses. For south-eastern Australian populations of Port Jackson sharks, growth curves and length-at-age relationships were calculated on the basis of the available sex-specific VBGF parameters (Ramos 2007; Tovar-Avi
cita et al. 2009b). Sex-specific comparisons of growth among regional populations of Port Jackson sharks were made using ANCOVA of the least-squares linear regression of the length-at-age data.

Data from Western Australia were also compiled, on the basis of reported maximum lengths of fish caught by commercial fishers (Jones et al. 2008, 2010). However, these data are limited to estimates of length at birth, sex-specific maximum lengths and lengths at maturity. Consequently, these data were used only to analyse spatial trends among regional populations of the species.

Results

Vertebræ analysis

Transverse vertebral sections possessed clearly identifiable concentric growth increments, which resulted in a high mean reader confidence of 3.44. Most vertebral centra had a readability score of 4 (confident: 44.5%) or 3 (moderate: 38.4%). No vertebrae were considered ambiguous or unreadable (<2); hence, no samples were excluded from the analysis. The high degree of reader confidence was reflected in the mean coefficient of variation and measure of precision of repeated counts of increments, being 4.65% and 3.29%, respectively. The mean IAPE for increment counts was 3.29% within established error thresholds (IAPE 5%; Campana 2001), indicating a high level of reproducible counts of vertebral increments.

The relationship between the D<sub>VC</sub> and L<sub>T</sub> was significantly linear (r<sup>2</sup> = 0.95, P < 0.0001), indicating that vertebral centrum growth is constant throughout life and that these structures are suitable for age determination for Port Jackson sharks.

Age estimation

Females ranged in ages from 0+ year, recently hatched individuals (based on the presence of signs of umbilical healing), to 18 years of age; whereas males ranged from 0+ to 16 years of age (Fig. 2). There was a lack of considerably larger, older individuals as seen in other age and growth studies of the species, presumably because of the size selectivity of the trawl sample-collection method used here.

Despite there being no significant difference in L<sub>T</sub> between the sexes (ANOVA: F<sub>1,179</sub> = 1.284, P > 0.05), growth parameters for the VBGF and the GGF were calculated for males and females separately, as well as for both sexes combined, to enable comparisons of growth rate between sexes. Both growth functions fitted the length-at-age data well (Table 1, Fig. 2), with females showing higher coefficients of determination (r<sup>2</sup> = 0.91) than males (r<sup>2</sup> = 0.87). Overall, the VBGF produced the largest estimates for asymptotic maximum length (L<sub>∞</sub>) and the lowest estimates of the growth coefficient (k) for males and females (Table 1).

For males, the VBGF provided a better fit to the length-at-age data than the GGF (Table 1, Fig. 2). The VBGF-derived values for L<sub>∞</sub> and k were 1069 mm L<sub>T</sub> and 0.094 years<sup>-1</sup>, respectively. These values differed considerably from those calculated by the GGF, as follows: L<sub>∞</sub> = 908 mm L<sub>T</sub> and k = 0.189 years<sup>-1</sup> (Table 1). Both the VBGF and GGF provided an equally good fit of the female length-at-age data (Table 1, Fig. 2). However, the resultant growth parameters differed markedly for each function, as follows: VBGF: L<sub>∞</sub> = 1266 mm L<sub>T</sub> and k = 0.082 years<sup>-1</sup>; and GGF: L<sub>∞</sub> = 1036 mm L<sub>T</sub> and k = 0.182 years<sup>-1</sup> (Table 1).
Comparisons of growth between sexes

Irrespective of the growth function applied to the length-at-age data, male Port Jackson sharks grew faster than their female counterparts (Table 1, Fig. 2), and significant differences between male and female VBGF curves were detected (ANCOVA: $F_{1,66} = 31.971, P < 0.001$). No significant difference was detected between the male and female GGF curves (ANCOVA: $F_{1,66} = 0.075, P > 0.05$).

Comparisons among regional populations

Significant differences were identified between sex-specific comparisons of VBGF growth curves among the three populations of Port Jackson sharks (Fig. 3), namely, New South Wales, Victorian and South Australian populations (ANCOVA: $F_{1,66} = 31.971, P < 0.001$). Differences among regional growth curves suggest the potential for population differentiation, with growth rates declining in an eastward direction, whereas $L_\infty$ remained relatively consistent among regions (Table 2, Fig. 4). The $L_\infty$ values presented for Western Australia are based on reported maximum lengths of animals caught by commercial fishers (Jones et al. 2008, 2010).

Discussion

Age estimation

Counts of growth increments in the vertebral centra provided a high degree of confidence for estimating the ages of Port Jackson sharks caught in South Australia. The resultant length-at-age data fit the von Bertalanffy and the Gompertz growth functions equally well; however, there were considerable differences in the calculated values of the growth rate between the two functions. In the majority of cases, the Gompertz-derived estimates of growth were twice those derived from the von Bertalanffy function. This discrepancy between these two growth models has been observed in other species of elasmobranchs, e.g. Chiloscyllium plagiosum (Chen et al. 2007), Carcharhinus plumbeus (Romine et al. 2006) and Isurus oxyrinchus (Natanson et al. 2006).

The Gompertz models fit the data well for both sexes, but provided a biologically unreasonable underestimate of maximum asymptotic length, subsequently overestimating the rate at which the asymptotic length of the species is attained (Romine et al. 2006). Although the Gompertz growth function is considered well suited to oviparous elasmobranch species, i.e. heterodontids (Cailliet and Goldman 2004), it may be better utilised in modelling elasmobranch weight-at-age data because of its sigmoidal shape and inflection point (Bishop et al. 2006). From herein, all reference to growth parameters will be in terms of the von Bertalanffy calculations.

Growth of the Port Jackson shark

Estimates of rates of growth for the Port Jackson shark indicated that the species is relatively slow growing in relation to other species of elasmobranchs (Branstetter 1987; Cailliet and Goldman 2004). Although species of elasmobranchs are characterised as possessing slow rates of growth, reported values of growth coefficients ($k$) among species are highly variable,
ranging from 0.30 to 1.337 (Cailliet and Goldman 2004). Rates of growth for the Port Jackson shark cannot be compared with other heterodontid species because analogous data do not exist; however, present findings are comparable to those reported for other populations of *H. portusjacksoni* (Ramos 2007; Tovar-Avila *et al.* 2009b).

Table 2. Comparisons of biological and von Bertalanffy growth parameters of the Port Jackson shark

<table>
<thead>
<tr>
<th>Parameter</th>
<th>WA 1</th>
<th>SA 2,3</th>
<th>Victoria 4,5</th>
<th>NSW 6,7,8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length at birth (mm <em>L_</em>&lt;sub&gt;b&lt;/sub&gt;)</td>
<td>180–210</td>
<td>170–212</td>
<td>295–315</td>
<td>211–345</td>
</tr>
<tr>
<td><em>L</em>&lt;sub&gt;∞&lt;/sub&gt; (mm <em>L_</em>&lt;sub&gt;b&lt;/sub&gt;)</td>
<td>1300F, 815M</td>
<td>1266F, 1069M</td>
<td>1242F, 1080M</td>
<td>1253F, 1119M</td>
</tr>
<tr>
<td><em>k</em> (year&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>n.a.</td>
<td>0.082F, 0.094M</td>
<td>0.070F, 0.084M</td>
<td>0.061F, 0.076M</td>
</tr>
<tr>
<td><em>t</em>&lt;sub&gt;0&lt;/sub&gt; (year)</td>
<td>n.a.</td>
<td>–1.64F, –2.19M</td>
<td>–3.86F, –4.09M</td>
<td>–3.58F, –4.07M</td>
</tr>
<tr>
<td>Female length at maturity (mm <em>L_</em>&lt;sub&gt;1&lt;/sub&gt;)</td>
<td>800–900</td>
<td>650–750</td>
<td>850–990</td>
<td>900–910</td>
</tr>
<tr>
<td>Male length at maturity (mm <em>L_</em>&lt;sub&gt;1&lt;/sub&gt;)</td>
<td>580–650</td>
<td>550–575</td>
<td>675–820</td>
<td>600–770</td>
</tr>
</tbody>
</table>

Fig. 3. Comparison of von Bertalanffy growth curves for (a) female and (b) male Port Jackson sharks from South Australia (solid line, the present study), Victoria (dashed line: Tovar-Avila *et al.* 2009b) and New South Wales (dotted line: Ramos 2007).

Fig. 4. Comparisons of estimates of rates of growth (*k*: △) and asymptotic total lengths (*L*<sub>∞</sub>: ○) for female (open symbols) and male (solid symbols) Port Jackson sharks (for sources of the data refer to Table 2). Western Australian total length data are based on maximum reported lengths.

The general pattern of growth depicted here is consistent with that observed in the Victorian population of the Port Jackson shark (Tovar-Avila *et al.* 2009b) and, more generally, in elasmobranch species (Cailliet and Goldman 2004). That is, the growth of the species is characterised by two distinct phases, including rapid growth at birth, which decreases around the time of sexual...
maturity (~600 mm $L_T$; Rodda and Svane 2007b), followed by a plateau in growth in the later years. These distinct bimodal phases were not readily apparent in New South Wales Port Jackson sharks, with juveniles and adults possessing comparable rates of growth (Powter and Gladstone 2008a). Generally, elasmobranch rates of growth differ considerably between adults and juveniles of the same species, as rapid juvenile growth is widely considered to be a survival mechanism that reduces predation on juvenile sharks (Branstetter 1990).

In line with previous studies, the South Australian Port Jackson shark displayed marked sexual dimorphism for rates of growth and estimated maximum lengths. Males were shown to have greater rates of growth than did females. In general, growth rates among elasmobranchs are extremely variable and show no correlation with size or geographic location. However, differences in rates of growth between sexes are common within species of sharks, with males generally possessing faster growth rates than females and achieving sexual maturity earlier (Cailliet and Goldman 2004).

Comparisons among regional populations
Francis and Francis (1992) cautioned against the direct comparison of individual von Bertalanffy parameters (i.e. $k$, $L_\infty$, and $t_0$) among populations, because they are highly correlated, with different combinations of values of the coefficients producing similar growth curves. Alternatively, they suggested that comparisons among actual growth curves are more appropriate. Direct comparisons of the von Bertalanffy growth curves of regional populations of Port Jackson sharks indicate that significant spatial differences exist. These findings support the theory of regional subpopulations of the species and are consistent with the available biological (i.e. reproductive biology: Tovar-Ávila et al. 2007) and ecological data for the species, e.g. tagging data (O’Gower and Nash 1978), allozyme variation (O’Gower and Nash 1978) and vertebral chemistry analysis (C. Izzo and B. M. Gillanders, unpubl. data).

Given that the Port Jackson shark is not generally retained for commercial purposes in spite of high catches, and maintains a high post-capture survivorship (Frick et al. 2010a, 2010b), there is little evidence to suggest that the observed differences in life histories are the direct result of fishing pressure. Conversely, these differences may be phenotypic responses brought about by variable environmental conditions experienced by these spatially separated populations (Begg et al. 1999b; Tovar-Ávila et al. 2007). This line of thinking aligns well with the philopatric behaviour demonstrated by the species and the lack of exchange of individuals among populations, even over relatively small spatial scales (Powter and Gladstone 2009). Tovar-Ávila et al. (2007) suggested that significant differences in a range of reproductive indices among subpopulations of Port Jackson sharks from western and far-eastern Victoria represent separate breeding populations in south-eastern Australia. The formation of reproductively isolated subpopulations may lead to genetic differentiation (Heist 2004b).

Yet, differences among estimates of individual growth parameters, particularly $k$ and $L_\infty$, because these two parameters are highly correlated, may be confounded by the sampling limitations of the different studies (Francis and Francis 1992; Pawson and Ellis 2005). The present study, like Tovar-Ávila et al. (2009b), employed a sampling methodology that precluded the capture of the largest size cohorts of the respective populations. The size selectivity of the trawl-fishing method employed in the present study failed to capture individuals >1000-mm $L_T$. The absence of larger, older cohorts may result in the underestimation of $L_\infty$ and the overestimation of growth (Francis and Francis 1992). Conversely, the absence of younger, smaller individuals (<2 years; <320-mm $L_T$) from the Victorian sample may further influence the estimated rate of growth for this population (Tovar-Ávila et al. 2009b).

On visual inspection of the sex-specific growth curves, little difference among length-at-age estimates at the middle and upper ends of the growth plots could be identified. Among regional populations of Port Jackson sharks, there was considerable overlap in the length ranges of size at birth and sizes at maturity among the four populations, such that no clear trends among the regional samples were evident. These findings do not support the idea that subpopulations are evident throughout the range of the species.

Clearly, identifying population structuring on the basis of biological and ecological data collated from a range of sources is problematic. Differences in methodology and samples among studies have the potential to confuse and confound the detection of real phenotypic differences among populations, limiting the ability to define the ranges of potential subpopulations. The use of highly variable molecular markers (i.e. microsatellite loci) is the logical next step to directly test for and delineate potential patterns of population division, connectivity and rates of gene flow throughout the distribution of the Port Jackson shark.

Conclusion
No clear pattern of population structuring for the Port Jackson shark was readily apparent on the basis of comparisons of life-history parameters among regional samples. Although significant differences were identified among regional growth curves, methodological limitations among studies potentially confound spatial comparisons. This was compounded by a lack of observable trends in the biological data among populations, thus failing to verify the statistically significant differences observed among regions.

Nevertheless, present findings indicate that the Port Jackson shark is a slow-growing relatively long-lived species. Moreover, this species has a low fecundity, producing on average 16 eggs per a breeding cycle (McLaughlin and O’Gower 1971) that are subject to extremely high rates of pre-hatch mortality (up to 89.1%; Powter and Gladstone 2008b). These factors could leave the species susceptible to population decline under exploitation, particularly because it has a low intrinsic rate of increase ($0.069 \text{ year}^{-1}$), coupled with a long generation time (22.5 years) and a low rebound potential (Powter and Gladstone 2008a). Yet, given the robust nature of the species to fishing activities (Frick et al. 2009, 2010a, 2010b), the egg-laying behaviour (Rodda 2000; Powter and Gladstone 2008c) and the fact that Port Jackson shark by-catch is not retained; this species may have a low risk of fisheries-induced population declines. This assessment of the susceptibility of the Port Jackson shark is consistent throughout the species range (Jones et al. 2008; Powter and
Gladstone 2008a; Tovar-Ávila et al. 2010). Because population structuring is not apparent, this generalised evaluation of resilience to decline could be cautiously assigned to regional populations throughout the distribution of the Port Jackson shark. However, robust genetic analysis is recommended to attain a direct assessment of this species population structure.

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