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Use of stochastic models to estimate the growth of the Port Jackson shark, *Heterodontus portusjacksoni*, off eastern Victoria, Australia

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ABSTRACT

Three stochastic models were used to describe the growth of *Heterodontus portusjacksoni* off eastern Victoria, Australia. The models are based on a reparametrization of the von Bertalanffy growth model to take account of length-at-age heterogeneity, and incorporate random variation of the von Bertalanffy growth coefficient (k), using three different probability distribution functions (*pdfs*): Weibull, gamma and log-normal. They were fitted to the lengths of 179 specimens (79 females and 100 males), and associated age estimates obtained by counting growth bands in the inner trunk dentine layer of the dorsal-fin spines. The species is relatively long-lived (maximum estimated age of 35 years for females and 28 years for males) and slow growing, but has rapid growth during the early stages of life. All the models provided similar growth parameters and length-at-age quantiles. However, Kullback's information mean indicated that the stochastic model assuming a log-normal distribution fitted the length-at-age data better for both females ($L\infty = 1337$, $E(k) = 0.059$, $t_0 = 5.294$) and males ($L\infty = 1125$, $E(k) = 0.075$, $t_0 = 4.944$) than the models assuming other distributions. The χ^2 likelihood ratio test indicated that females and males grow differently.

1. Introduction

The description of somatic growth is a basic problem in population biology (Francis, 1988a). Growth rate is essential for some dynamic population models useful in determining sustainable yields of exploited species, such as yield per recruit models (Francis and Francis, 1992). Age and growth also provide a basis for the estimation of other important population parameters, such as mortality rate and longevity, necessary for assessment and management of a population (Natanson et al., 2002). Some biological variables (proportion of population mature or in maternal condition, litter size, mass) are commonly expressed as a function of the length of fish, but their expression as a function of age is necessary for demographic and other standard assessment models. Thus, confident estimates of population parameters that depend on age and growth, and confident demographic and fishery assessment using such particular parameters depend on accurate determinations of age and reliable estimates of somatic growth rates.

Several functions have been developed to describe the somatic growth of fish, of which the von Bertalanffy (1938) growth model (VBGM), later applied to fisheries data by Beverton and Holt (1957), is the most commonly adopted (Cailliet and Goldman, 2004). The VBGM derived from an analysis of the physiological process involved in organic growth, specifically the relationship between anabolism and catabolism (von Bertalanffy, 1938). Another convenience of the VBGM is its wide use, allowing comparisons with growth curves from other populations. However, biological interpretation of the VBGM parameters has been questioned because the values of two of its parameters (L_∞ and t_0) inevitably fall outside the range of data (Francis, 1988a, 1988b; Francis and Francis, 1992), because has a limited ability to describe growth if the length-at-age data are not extensive enough to demonstrate asymptotic growth (Knight, 1968; Francis, 1988b), and because it is not suitable for data from tagging experiments (Francis, 1988a). To provide a more flexible and biologically comprehensive representation of growth, a stochastic variation of the VBGM has been developed (Troynikov, 1998). This stochastic approach can explicitly account for both heterogeneity in length-at-age and measurement error by incorporating random variation in one or more of its parameters. Ignoring such heterogeneity can result in biased estimates of the growth parameters (Sainsbury, 1980).

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The Port Jackson shark, *Heterodontus portusjacksoni* (Meyer, 1793), is a demersal species endemic to southern Australia (Last and Stevens, 1994), commonly caught as bycatch in several fisheries (Walker et al., 2005). Observations of captive *H. portusjacksoni* indicate that the species grows slowly. Juveniles grow 5–6 cm per year and adults grow 2–4 cm per year (McLaughlin and O'Gower, 1971). However, no attempt has been made to determine growth parameters by ageing animals caught from the wild. The aim of the present study was to determine the growth parameters for *H. portusjacksoni* from eastern Victoria, Australia, using the stochastic VBGM to take into account heterogeneity in age-at-length data. Age estimates derived from counts of growth bands in the inner trunk dentine layer of dorsal-fin spines from an extensive size range allowed fitting the stochastic models. Although full age validation for *H. portusjacksoni* has not been achieved, the periodicity of growth band formation in dorsal-fin spines has been validated by using oxytetracycline and other fluorescent markers in captive and wild females from 377 to 970 mm TL (apparent ages from 1 to 18 years) and wild males from 430 to 660 mm TL (3–12 years) (Tovar-Ávila et al., 2008). Enamel bands form annually in the cap of the spines of this species, whereas pairs of alternating opaque (summer) and translucent (winter) growth bands form annually in the trunk dentine layers of the spine, with the first band probably corresponding to the birth mark. Counts of growth bands in the inner trunk dentine layer have also been verified by using multiple readers and by comparing them with counts from the cap of the spine and other calcified structures such as vertebrae (Tovar-Ávila, 2006).

2. Materials and methods

2.1. Sampling and tissue processing

Specimens of *Heterodontus portusjacksoni* were caught by commercial fishers in eastern Victoria (Mallacoota and Point Hicks), Australia, using gillnets of 6 1/2-in. mesh-size. The sharks were kept on ice after capture and transported to the laboratory in Queenscliff, where they were measured and dorsal-fin spines collected and processed. Total length (TL) was measured to the nearest 1 mm as a straight line from the tip of the snout to the distal end of the tail, while the shark was in a natural position without stretching it. A subsample of 200 sharks (100 females and 100 males) was randomly selected from ~400 sharks collected, except that the largest and smallest animals were selected to include the minimum and maximum sampled lengths. The dorsal-fin spines were obtained by cutting them to their base over the vertebral column. For sharks where the first spine was extensively damaged the second dorsal-fin spine was obtained, as both structures have been shown to provide similar growth band counts (Tovar-Ávila, 2006). The dorsal-fin spines were cleaned with a scalpel and washed in tap water. After cleaning, the spines were air-dried and stored in labelled paper envelopes. Cross-sections of the spines (~300 μm thick), at the level where the pulp cavity remains open, were cut using a lapidary saw (Gemmasta®) after embedding the structures in polyester resin. The sections were mounted on glass microscope slides and sealed with cover slips.

2.2. Age determination

A growth band comprised a pair of translucent and opaque zones in the inner trunk dentine layer of the dorsal-fin spines. Growth band counts were made from the pulp cavity towards the trunk primordium, identified as the point were the blood vessels or canaliculi merge (Fig. 1). The dorsal-fin spine terminology used follows Maisey (1979) as this proved to be consistent with the spines external and internal structure, whereas the age and growth related terms used follow in general Clarke and Irvine (2006). Growth bands before or after any discontinuity (identified as a check crossed by the canaliculi) were included in the counts, as only two trunk dentine layers (inner and outer) have been found in the spines of *H. portusjacksoni* (Tovar-Ávila et al., 2008). Three sets of independent counts of the growth bands were made under a dissecting microscope for each sample without prior knowledge of the animal length, sex or previous band counts, following Irvine et al. (2006). The counts were undertaken with a minimum of one month between them to avoid the count being influenced by the previous one. Where one of the counts disagreed, a fourth count was made and the number of growth bands was accepted if three counts agreed. Where all four counts disagreed, but the difference in counts was low (Average percent error between counts of the sample, APE < 1%), the sample was reread again to assign the most probable number of growth bands. Samples where all four counts disagreed and difference in counts was high (APE > 1%) were rejected from further analysis. The readability of growth bands was ranked according to their clarity of growth bands using a scale modified from Officer et al. (1996) (Table 1). Only age estimates from dorsal-fin spines with a readability score ≤3 were included in the analysis.

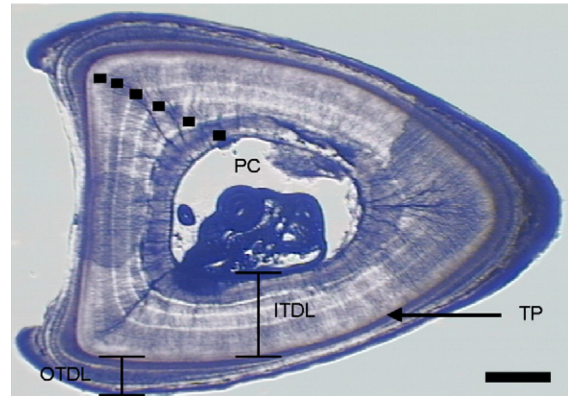

Fig. 1. Growth increment bands (represented with dark dashes) in a sagittal section of the inner trunk dentine layer (ITDL) of a sectioned dorsal-fin spine (female 556 mm TL) of *Heterodontus portusjacksoni*. PC = pulp cavity; OTDL = outer trunk dentine layer and TP = trunk primordium. Scale bars = 0.5 mm.

The age of sharks was determined from the number of band counts and the date of capture. Because *H. portusjacksoni* eggs commonly hatch during winter (end of June–end of August in the Southern Hemisphere), 1 July was arbitrarily set as the date of birth for all sharks. The age of a shark (in years) was then calculated as the number of complete growth bands (a translucent zone followed by an opaque one) less one (birth band) plus t divided by 365, where t is the number of days between the previous 1 July and the date of capture.

Table 1
Readability score (modified from Officer et al., 1996).

Score	Description
1	Growth band count unambiguous with exceptionally clear bands
2	Growth band count unambiguous but bands of diminished clarity
3	Two growth band counts possible but indicated count is most likely
4	More than two interpretations possible; growth band count is best estimate
5	No growth band count possible; unreadable