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Age, growth, and reproduction of the Roughtail Skate Bathyraja trachura (Gilbert, 1892) from the eastern North Pacific

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AGE, GROWTH, AND REPRODUCTION OF THE ROUGHTAIL SKATE *BATHYRAJA TRACHURA* (GILBERT, 1892) FROM THE EASTERN NORTH PACIFIC.

A thesis submitted to the faculty of
Moss Landing Marine Laboratories and
California State University Monterey Bay
in partial fulfillment of
the requirements for
the degree

Masters of Science
in
Marine Science

by

Chanté Davis
May 2006

CERTIFICATION OF APPROVAL

I certify that I have read “Age, growth, and reproduction of the roughtail skate, *Bathyraja trachura* (Gilbert 1892) in the eastern North Pacific” by Chanté Davis, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirements for the degree: Master of Science: Marine Science at California State University, Monterey Bay, Moss Landing Marine Laboratories (MLML).

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ABSTRACT

Age and growth characteristics of the roughtail skate *Bathyraja trachura*, a poorly-known deep-water species, were determined from samples collected along the continental slope of the contiguous western United States. A new maximum size was established at 91 cm TL. Age was estimated using a traditional structure (vertebral thin sections) and an alternative non-lethal structure (caudal thorns). Based on poor precision and significantly lower age estimates when compared to age estimates from thin sections, caudal thorns were determined not to be a useful ageing structure for this species. Age estimates from vertebral thin sections were used to model growth. Annual band deposition was found to be a reasonable assumption for this species, but was not validated. Assuming annual band deposition and using length-at-age data, the best model for describing growth of *B. trachura* was the two parameter VBGF, (L_∞= 101.25, k = 0.09). Although females grew slower and reached a larger maximum size than males, their growth parameters were not statistically different therefore data were pooled (ARSS; $p = 0.78$). The maximum age determined for *B. trachura* was 20 yrs for males and 17 yrs for females using vertebral thin sections. First and 50% maturity occurred in males at 58.0 cm TL (~11 yrs) and 72.0 cm TL (~14 yrs). First and 50% maturity occurred in females at 58.0 cm TL (~7 yrs) and 77.0 cm TL (~ 13yrs). Gonosomatic and hepatosomatic indices did not indicate a seasonal trend of the reproductive cycle, suggesting that reproduction may be year round.

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INTRODUCTION

In Californian waters, skates are directly targeted and taken incidentally as bycatch in commercial fisheries (Martin & Zorzi 1993). Landing records often report skate species as "unidentified skate," thus preventing an assessment of the potential effects of fishing on population dynamics (Zorzi et al. 2001). Determining the impact of fishing mortality on exploited skate populations is further hindered by a lack of species-specific life history information (Holden 1972, Martin & Zorzi 1993, Stevens et al. 2000, Dulvy & Reynolds 2002). This is of concern because some skates have life history characteristics (e.g. slow growth, late age at maturity, low fecundity, and moderate longevity) that make them susceptible to overfishing (Holden 1972, Stevens et al. 2000, Dulvy & Reynolds 2002). If current trends continue, fishing effort on skates is likely to increase, subjecting these vulnerable fishes to possible overexploitation.

Fishing mortality has been associated with the declines of many skate populations worldwide. Walker & Hislop (1998) reported that relative abundance of skate species in north-east Atlantic waters was once dominated by the late-maturing blue skate (*Dipturus batis*). However, because of fishery exploitation, the skate assemblage is now dominated by the early-maturing thorny skate (*Amblyraja radiata*). Fishing mortality has also contributed to population declines in the north-west Atlantic of the winter skate (*Leucoraja ocellata*), barndoor skate (D. *laevis*), blue skate (*D. batis)* (Johnson 1979, Brander 1981, Casey & Myers 1998). Knowledge of life history parameters and how they influence population dynamics of individual species is needed to better understand the impact of fishing mortality and to better develop appropriate management strategies.

Fishery biologists incorporate age and growth information into models to analyze the population dynamics of individual species (Campana 2001). Ages of chondrichthyans can be estimated using a traditional structure (thin sectioned vertebrae) and a second more novel and non-lethal structure (caudal thorns) (Gallagher and Nolan 1999). The calcified vertebral centra of elasmobranchs contain a pattern of opaque and translucent bands which have been found in many species to form during summer and winter months respectively (Cailliet and Goldman 2004). The thorns are similar to placoid scales in that they are composed of three layers (Gallagher and Nolan 2005). A pulp core forms the inner layer, followed by a dentine middle and finally a vitrodentine outer layer. Unlike vertebrae, caudal thorns do not support mass; their growth may not be inherently linked with somatic growth. Gallagher and Nolan (1999) attempted to investigate the use of caudal thorns as an ageing structure but few studies have attempted to evaluate age estimates between these two structures (Cailliet and Goldman 2004).

Reproductive seasonality of chondrichthyans is typically evaluated using the gonosomatic (GSI) and hepatosomatic (HSI) indices. Traditionally, gonad indices were used to analyze reproductive development. Lipids are metabolized in the liver as gamete production ensues leading to an inverse relationship between GSI and HSI (Nikolsky 1963).

Bathyraja trachura is a poorly-known eastern North Pacific (ENP) skate that is common at depths of 213 - 2,550 m and may be vulnerable to bycatch in trawl fisheries. It is one of six representatives of the genus *Bathyraja* (Family: Arhynchobatidae) reported from the ENP from the Bering Sea to northern Baja California (Ebert 2003).

Information about this species in ENP waters is sparse and limited to taxonomic guides and a few descriptions of egg cases and advanced embryos (Cox 1963, Ishihara and Ishiyama 1985, Zorzi and Anderson 1988, Craig 1993, Ebert 2003, Ebert and Davis *in review*).

To address this knowledge gap, I estimated age, calculated population growth parameters and determined seasonality of the reproductive cycle for *B. trachura* in ENP waters. Results provided age and growth data that are necessary to model growth and will provide valuable information about the reproductive cycle that is necessary for determining age and size at maturity. The results will provide previously unknown but critical life history information for the formulation of an effective management plan for *B. trachura* in the ENP.

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Chapter 2: Age and growth of the roughtail skate, *Bathyraja trachura*

INTRODUCTION

Fishery biologists incorporate age and growth information into models to analyze the population dynamics of individual species (Campana 2001). Early age and growth research focused on skates because of their abundance, hardiness and ability to survive in captivity, but was limited to nearshore species such as the black-skate (*Raja fusca*), yellow-spotted skate (*R. hollandi*), thornback skate (*R. clavata*), blonde skate (*R. brachyura*), spotted skate (*R. montagui*), and smalleyed skate (*R. microocellata)* (Ishiyama 1951, Holden 1972, Ryland and Ajayi 1984). Since these early studies fishing pressure in some areas has increased motivating research into the life history of these poorly understood species (Casey and Meyers 1998, Cailliet and Goldman 2004).

Sharks, skates and rays lack otoliths, therefore other calcified structures such as vertebral centra, neural arches, spines and caudal thorns are used in age determination (Holden and Meadows 1962, Cailliet et al. 1983, Cailliet and Tanaka 1990, Gallagher and Nolan 1999, Cailliet and Goldman 2004, Serra-Pereira et al. 2005). These structures contain a pattern of opaque and translucent bands that have been found in many species to form during summer and winter months, respectively. However, this assumption must be validated for each species to ensure accurate estimates of age (Campana 2001, Cailliet and Goldman 2004).

The objectives of my study were to provide estimates of age and describe growth characteristics for *B. trachura* in eastern North Pacific (ENP). Specifically, I estimated size-at-age for *B. trachura* using age estimates from vertebral thin sections and caudal thorns. Centrum edge and marginal increment analysis (MIA) were applied as age validation techniques and growth models were generated using length- and weight-at-age data for each sex.

MATERIALS AND METHODS

Specimen Collection

Skates were obtained from along the Pacific coast of the contiguous United States between 48.6 ° and 33.35° north latitude (Figure 1). Samples were collected in summer and fall 2002-2003 during the Northwest Fisheries Science Center annual groundfish surveys. Additional samples were collected during winter and spring 2004 from commercial fishery landings via the Pacific States Marine Fisheries Commission - West Coast Groundfish Observer Program.

Sex was determined for each specimen, vertebrae and caudal thorns were removed, and biological information was recorded. Total length (TL), disc length (DL), and disc width (DW), were measured to 0.1 cm and total weight (kg) was recorded following Hubbs and Ishiyama (1968). The first eight vertebrae and first six caudal thorns were removed from each specimen and frozen prior to analysis.

Preparation and evaluation of ageing structures

Vertebral columns were cleaned of extraneous tissue with a scalpel, neural and haemal arches were removed and individual centra were separated. To be a useful aging structure, vertebral centra must grow predictably with TL. Mean vertebral centrum diameter was calculated from two measurements across the dorsal/ventral and lateral axes to the 0.01 mm (Figure 2). Mean centrum diameter was plotted against TL and a linear regression was used to determine the relationship between vertebral growth and somatic growth.

Whole vertebrae were embedded in a polyester casting resin. A 0.3 mm thin section containing the nucleus was removed using a Buehler Isomet low speed saw with paired 10 cm Norton diamond-edged blades. Thin sections were mounted on slides with Cytoseal 60 and polished using 1200 grit wet sandpaper, and viewed under a dissecting scope with transmitted light. A pilot study comparing the application of band enhancement techniques following Gruber and Stout (1983 and Gallagher and Nolan (1999) proved that unstained thin sections provided the best band clarity.

All trunk centra from 11 specimens were removed and used to verify consistency of age estimates throughout the vertebral column. Age estimates of the first five vertebrae from the anterior part of the column were compared to age estimates from the last five vertebrae from the posterior part of the column. A paired t-test was used to determine if mean age estimates differed significantly (Zar 1999).

Caudal thorns were manually trimmed of extraneous tissue (Goldman 2004). Whole thorns were then submerged in 3.0 % trypsin soak for 48 – 72 hours to remove remaining tissue (Gallagher and Nolan 1999). A subsample of caudal thorns were partially embedded in a fiberglass resin and sectioned laterally. A banding pattern was not apparent on sectioned thorns therefore, age was determined from whole caudal thorns for remaining samples. Whole thorns were placed on slides at 30° – 50° angle and viewed under a dissecting scope with transmitted light.

To determine if caudal thorns would be a useful ageing structure, structural growth, consistency of age estimates, and the potential for thorn replacement were evaluated. Caudal thorn base diameter, measured along anterior-posterior thorn axis, and height was measured from protothorn tip to caudal thorn base using dial calipers to 0.1 mm (Figure 2). Measurements were plotted against TL to determine the relationship between caudal thorn size and body size. A pilot study comparing the application of band enhancement techniques following the methods of Gruber and Stout (1983) and Gallagher and Nolan (1999) proved that unstained thin sections provided the best band clarity. Age estimates determined during the pilot study were not included in final analysis.

All caudal thorns were removed from the tail of 11 specimens and used to evaluate consistency of age estimates along the tail. Age estimates from the five anterior most caudal thorns were compared to age estimates from last five posterior most caudal thorns. A paired t-test was used to determine if mean age estimates differed (Zar 1999). To determine the potential for thorn replacement, caudal thorns were counted on each specimen and plotted against TL. A linear regression was used to determine the relationship between thorn count and somatic growth.

Age determination and validation

The birthmark in each vertebral centrum was identified as the change in angle of the corpus calcareum and was located on thin sections through all size classes (Cailliet and Goldman 2004) (Figure 3). Banding patterns were not enhanced using the methods described, therefore thin sections were processed unstained. Each opaque and translucent band pair was considered to represent as one year of growth.

A sample of 100 caudal thorns, representing all size classes, was selected for analysis using stratified random sampling. Four were damaged, leaving a total of 96 caudal thorns (51 females, 45 males) for age analysis. The birthmark, identified on caudal thorns though all size classes, was identified as a distinct ridge at the base of the protothorn (Cailliet and Goldman 2004) (Figure 3). The protothorn forms the tip of the caudal thorn and lacks growth bands. Each translucent and opaque band was considered to represent of one year of growth.

Age estimates were determined using three rounds of independent age estimates by one reader without advanced knowledge of length, season of capture, or sex of the sample. If agreement was not achieved among these three estimates, a fourth read was completed. If agreement was not achieved by the fourth read, samples were removed from analysis. A clarity grade was assigned to each sample based on criteria adapted from Officer et al. (1996). Grade 1: bands were clear and distinct; grade 2: bands were clear but not distinct; grade 3: two band counts were possible and the better estimate was recorded; grade 4: bands were blurry and more than two band counts were possible therefore the best estimate was recorded; and grade 5: poor clarity resulted in a band count that was not confident. Samples receiving a poor clarity grade were removed from analysis.

Age estimates were evaluated for reader precision and structural bias. Precision among age estimates was assessed using average percent error (APE) (Beamish and

Fournier 1981), coefficient of variation (CV) and the index of precision (D) (Chang 1982). Percent agreement (PA) was calculated to determine precision of age estimates between rounds and was evaluated for exact agreement, agreement within one year, and within two years of age (Cailliet and Goldman 2004). Age-bias plots were used to determine the potential bias of age estimates within and between each independent read and between structures (Campana et al. 1995). A pair-wise comparison of age estimates was plotted against a 1:1 age bias line demonstrating perfect agreement. An age estimate above the line represents bias toward older ages whereas an age estimate below the line represents bias toward younger ages by read x over y (Campana et al. 1995). Error bars were calculated for ± standard error.

Final age estimates were compared between vertebrae and caudal thorns from the same animal. Precision and bias were calculated as previously described to evaluate variation of age estimates between structures. A paired t-test was used to determine if there was a significant difference between mean age estimates (Zar 1999).

Validation, using vertebral thin sections, was attempted using edge analysis and marginal increment ratio (MIR) (Hyndes et al. 1992, Campana 2001). Edge analysis is an optical classification of a thin sections' outermost band as opaque or translucent. Alternately MIR is a measured ratio representing the relative completion of the newest deposited band in comparison to the previous band pair and was calculated as:

$$MIR = MW/PBW$$

where MW is margin width and PBW is previous band width (Figure 4) (Conrath et al. 2002). The resulting ratios were plotted against month of collection to determine the periodicity of band deposition (Cailliet and Goldman 2004). Equality of variances was determined using Cochran's test, following which an ANOVA was used to test for seasonality of band deposition (Zar 1999).

Growth

The von Bertalanffy (VBGF) and Gompertz growth functions were fitted to length- and weight-at-age data for both sexes. The parameter estimates for each function were estimated using SigmaPlot version 8.0 (SPSS Inc., 2002). To determine if growth differed between sexes, analysis of the residual sums of squares (ARSS) was calculated (Chen et al. 1992, Haddon 2001).

The VBGF was fitted to length-at-age data and was calculated as:

$$l_t = L_\infty(1 - e^{-k(t-t_o)})$$

where l_t is the predicted length at age t, L_∞ is the maximum length predicted by the equation, k is the growth coefficient, t_o is the theoretical age at which length is zero (Beverton & Holt 1957). Fabens (1965) incorporated known size at birth to better reflect biological reality. A two parameter VBGF with a fixed length at birth (L_o) was calculated as:

$$l_t = L_\infty - (L_\infty - L_o)e^{(-kt)}$$

where l_t is the predicted length at age t, L_∞ is the maximum length predicted by the equation, k is the growth coefficient and L_o is set to the known length at birth (19.0 cm). A von Bertalanffy growth function fitted to weight-at-age data following Fabens (1965) and Ricker (1979) was also applied:

$$W_t = W_\infty(1 - e^{-k(t-t_0)})^3$$

where W_∞ is the theoretical asymptotic weight, and values for k, t, t_0 are the same as previously described. The Gompertz function (Ricker 1979) was fitted to weight and length-at-age data:

$$W_t = W_\infty e^{(-ke^{-gt})}$$

where W_t is age, t is estimated age, g is the instantaneous growth coefficient, k is a dimensionless parameter and the other parameters are as previously described. To evaluate goodness-of-fit, the standard estimate of the error (SEE) and plots of standardized residuals were evaluated (Cailliet et al. 1992). Model selection was based on statistical fit (r^2), convenience, and biological relevance.

RESULTS

Sample collection

In total, vertebral centra of 231 specimens (102 females, 129 males) and caudal thorns of 100 specimen (54 females, 46 males) were used for age estimation. The smallest female was 14.5 cm TL and male was 16.0 cm TL. The largest female was 86.5 cm TL and male was 91.0 cm TL (Figure 5).

Preparation and evaluation of ageing structures

Vertebrae were determined to be a useful ageing structure based on a positive linear relationship between the structure and TL (Figure 6). There was no significant difference of centrum size between sexes ($F_{0.05,1,206} = 1.665$, $p = 0.198$); therefore, values were pooled for analysis. A positive linear relationship was identified between TL and centrum diameter ($n = 231$, $y = 0.071x - 0.2402$, $r^2 = 0.92$, $p<0.01$).

Whole vertebral columns were removed from 11 specimens to determine if age was consistent throughout the structure however, clear age estimates were only available in anterior and posterior vertebrae from nine specimens. There was no significant difference between age estimates from anterior and posterior vertebral thin sections ($n = 9$, $t_{(0.05(2),8)} = 0.748$, $p = 0.47$) (Figure 7). All age estimates were based on anterior vertebral centra.

The utility of caudal thorns as ageing structures was not demonstrated (Figure 8). Caudal thorn size increased with body size, there was no evidence of thorn replacement, and ages were consistent along the tail. A logarithmic curve represented the best fit between thorn height and total length ($n = 100$, $y = 0.6737\text{Ln}(x) + 0.3329$, $r^2 = 0.24$) and between thorn base length and total length ($n = 100$, $y = (2.4073 * \text{Ln}(x)) - 5.652$, $r^2 = 0.60$) (Figure 8a). Meristic counts of caudal thorns (from 248 additional specimen not aged in this study) indicated caudal thorn count and TL were not significantly related ($y = -0.0266x + 26.91$, $r^2 = 0.04$, $p<0.01$) (Figure 8b).

The presence of healed scars suggests that thorn replacement does not occur in this species. Additionally, there was no significant difference between age estimates from anterior and posterior caudal thorns ($t_{(0.05(2),7)} = 1.62$, $p = 0.15$). Therefore, age was estimated from anterior caudal thorns (Figure 9).

Age determination and validation

Final age estimates were determined from 197 vertebral samples which provided the best band clarity. Analysis of vertebral band clarity grades indicated that visibility of bands was variable and inconsistent between samples. Few (13.8%) were graded as clear with distinct bands (grade 1). The majority (69.0%) received grade 2 or 3, indicating that bands were clear and the best estimate was recorded. Another 6.9% received grade 4. Approximately 9.6% were determined to be of poor clarity (grade 5) and were not included in analysis.

Calculations of bias and precision indicated the first round of vertebral band counts was biased toward older age estimates (Table 1). Average percent error and coefficient of variation were acceptable between the three independent rounds of band counts (APE: 13.57%, CV: 18.62 %, D: 9.31). Percent agreement within two years was 76.1% and 67.51% respectively, for first vs. second and first vs. third rounds of band counts. Greater agreement was found between the second and third round of band counts (86.8%). Age-bias plots indicated that the first round of band counts were biased toward older age estimates (Figure 10).

Caudal thorn samples that received poor clarity grades (2.0%) were removed from analysis and final age was determined for 96 samples. Analysis of clarity grades indicated that visibility of bands were variable and inconsistent between samples. Several (26.7%) were graded as clear with distinct bands (grade 1). The majority (56.7%) received grade two or three, indicating that bands were clear or foggy and the best estimate was recorded. Another 13.3% received grade 4 and approximately 2.2%

were determined to be of poor clarity (grade 5). Only samples with clear banding and acceptable clarity ratings were used in analysis.

Precision and bias indicated that the first round of band counts had the greatest variation (Table 1). Average percent error and coefficient of variation values for caudal thorns were highest when all rounds of band counts were combined (APE:17.7%, CV: 24.6%, D:12.3). Percent agreement calculations also indicated that the second and third round of band counts were most similar, 82.2% within two band counts. Age bias plots indicated that the first round of band counts produced greater bias when compared to later rounds, indicating that reader ability improved over time (Figure 11).

Vertebral thin sections were determined to be a better structure than caudal thorns for age estimation of *B. trachura*. Age estimates between the structures were consistent until age 7 and then became quite variable (Figure 12). Age estimates compared between structures produced unacceptable precision values and bias (APE: 29.9 %, CV: 40.4 %, D: 28.5). There was a significant difference between ages estimated from vertebral thin sections and those estimated from caudal thorns ($t_{0.05(2)17} = 3.003$, $p = 0.007$). Age estimates of vertebral thin sections were more precise, and were used for validation and growth analyses. The maximum ages determined by estimates from vertebral thin sections were 17 yrs (females) and 20 yrs (males).

Band deposition could not be validated using the methods applied in this study. Thirty-five percent of thin sections were removed from edge analysis because of poor clarity of the thin section. Edge analysis did not show a significant difference between the occurrence of opaque and translucent bands among months ($\chi^2_{0.05,3} = 1.06$, $p<0.75$)

(Figure 13). Likewise, seasonality of band formation could not be validated using MIR. Sixty-five percent of thin sections were of optimal clarity and used for MIR analysis. There was no significant difference between MIR values among seasons ($F_{0.05,10,128}$ = 0.75, p =0.67) (Figure13). Although validation was not achieved using edge and MIR analysis, growth models were derived assuming annual deposition of one opaque and translucent band.

Growth

Multiple growth models were fitted to length-at-age and weight–at–age data (Cailliet et al. 2006) (Figure 14). The model providing the most biological reasonable fit for the data was the 2 parameter VBGF. Functions fitted to weight-at-age data provided poor statistical fit (Gompertz: $r^2 = 0.74$, VBGF: $r^2 = 0.79$). Growth functions fitted to length-at-age data provided good statistical fit. Fit was similar for the three parameter VBGF ($r^2 = 0.93$), two parameter VBGF ($r^2 = 0.92$) and Gompertz (total length, $r^2 = 0.92$) growth functions (Table 2). The three parameter VBGF generated the largest estimate of L_∞ (112.11 cm) and the lowest growth coefficient (k = 0.06) however, the plot overestimated known size at birth. The Gompertz provided the lowest L_∞ (92.62 cm) and largest growth coefficient (k = 1.37) however, the plot also overestimated known size at birth (Figure 14). The two parameter VBGF predicted a reasonable L_∞ (101.25) and was set at the appropriate birth size, therefore it was the most biologically reasonable function.

Females reached a larger maximum size ($L_\infty = 101.53$) at a slightly slower rate ($k = 0.08$) than males ($L_\infty = 100.17$, $k = 0.09$). However, there was no significant difference between female and male growth ($F_{0.05,1,197} = 0.03$, $p = 0.78$). Therefore, data were combined and the resulting growth parameters for the pooled two parameter VBGF were $L_\infty = 101.25$ cm and $k = 0.09$.

DISCUSSION

This study expanded the known size range of *B. trachura* to include a new TL_{max}, one adult male was measured at 91.0 cm TL. Prior to this study the birth size was estimated at 14.2 cm TL and maximum size was 89.0 cm TL (Ishihara and Ishiyama 1985, Craig 1993). Samples were obtained from commercial fisheries and fishery-independent surveys, but neither source used trawling gear that could sample the entire depth range of this species; it is possible that larger specimen exist.

Caudal thorns were not determined to be a valid structure for age estimation of *B. trachura.* Caudal thorns of *B. trachura* did not grow linearly with body size, suggesting that their growth slowed with increased size and age estimation of larger individuals would be difficult (Francis & Maolagáin 2005). Caudal thorn height was difficult to relate to TL because of protothorn erosion in larger specimens. Because thorns originate from dermal dentical scales and, unlike vertebrae, do not support mass; thorn growth may not be inherently linked to somatic growth (Gallagher et al. 2005). Caudal thorns were originally considered as a possible ageing structure for this study because of the consistency of age estimates throughout the structure. Subsequent evaluation of precision proved that age estimates from thorns were not precise. Maximum ages determined by caudal thorns were less than half the maximum age determined by vertebral thin sections. Bias between the structures was unacceptable.

Gallagher and Nolan (1999) first used caudal thorns as an ageing structure for four species of *Bathyraja* from the Falkland Islands: *B. brachyurops*, *B. griseocauda*, *B. scaphiops*, and *B. albomaculata*. Caudal thorns were found to be suitable ageing structures that provided precise age estimates and ease of band interpretation. Since their publication caudal thorns often have proven to be a difficult structure to age, producing poor precision (Francis & Maolagáin 2005) and may be complicated by the slowing of thorn growth with increased somatic growth (Perez 2005). Perez (2005) also found evidence of thorn replacement in *B. kincaidii*, indicating that not every thorn depicted actual age for this species.

Seasonality of band pair deposition in vertebral thin sections could not be validated using MIR and edge analysis. Diminished clarity of the banding pattern was caused by poor calcification of the vertebral edge, distortion of edge quality caused by overpolishing or inability to acquire a clear photographic image of the region. This lack of clarity limited the number of samples included in MIR, potentially restricting detection of band periodicity.

Although vertebral band deposition was not validated, standard age determination methods were applied to a commonly used ageing structure. Vertebral thin sections have been used for ageing more than 67 elasmobranch species (Cailliet and Goldman 2004, Perez 2005, McFarlane and King 2006, Licandeo et al. 2006). Among these studies, annual band deposition was validated for 54 species including seven skate species (Cailliet and Goldman 2004, Licandeo et al. 2006). These findings lend support to the assumption of annual band deposition used to determine age for *B. trachura*. However, caution is necessary when using unvalidated age estimates for management purposes because of the inherent possibility for over or underestimation of age. (Campana 2001, Cailliet and Goldman 2004).

In this study the criteria used for growth model selection were statistical fit, convenience, and biological relevance (Table 2). Growth functions fitted to weight-at-age data provided the lowest variance about the mean, however W_∞ was underestimated by both functions ($W_{max} = 5.0$ kg). The two parameter VBGF, fitted to length-at-age data, estimated a reasonable L_∞ and was the only length model which did not overestimate L_0 making it the most biologically reasonable choice. Since the three parameter VBGF is the most commonly applied model for elasmobranch species (Cailliet and Goldman 2004) these values are used for comparison with the published literature.

The predicted growth parameters for *B. trachura* are not consistent with the assumption that larger batoids live longer and grow slower than smaller batoids. *Bathyraja trachura* is a medium sized species (91 cm) with a growth coefficient ($k = 0.06$) that is smaller than some smaller relatives such as *B. kincaidii* ($k = 0.21$, Perez 2005) but not some others like *Raja clavata* ($k = 0.05$, Brander and Palmer 1985) (Table 3). Maximum age of *B. trachura* was determined to be 20 yrs, which is older than smaller species but not younger than all larger species such as *Amblyraja radiata* (16 yrs, Sulikowski et al. 2005) (Table 3).

This study provides the first published age estimates for *Bathyraja trachura*. In summary the two parameter VBGF, assuming annual band deposition and using length-at-age data, is the most biologically reasonable function to describe growth for *B. trachura*. Females and males did not significantly differ in their growth. Annual band deposition was assumed to be a reasonable assumption for this species, but has yet to be validated. Caudal thorns were determined not to be a useful ageing structure for this species based on high precision values and significantly lower age estimates when compared to age estimates from thin sections.

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Table 1: Precision values for final age estimates of vertebral thin sections and whole caudal thorns for *Bathyraja trachura*

Precision	Vertebrae	Caudal Thorns	Structural Comparison
APE (%)	13.57	17.7	29
CV (%)	18.62	24.6	40.3
D (%)	9.31	12.3	27.8
PA ±0 (%)	32.5	15.8	-
PA ±1 (%)	70.1	60.4	-
PA ±2 (%)	86.8	82.2	-

Table 2: Growth functions and estimated parameters for *Bathyraja trachura*. Length and weight-at-age data are represented for sexes combined. Note: SEE = standard error of the estimate, VBGF = von Bertalanffy growth function, t_o = size at birth, k and g = growth coefficients, $L_o(W_o)$ = size(weight) at birth, $L_\infty\ (W_\infty)$ = maximum size(weight).

	Length-at-age			Weight-at-age	
Parameter	3 Parameter VBGF	2 Parameter VBGF	Gompertz	VBGF	Gompertz
$L_\infty\ (W_\infty)$	112.11	101.25	92.62	(3.23)	(3.22)
$L_o(W_o)$	22.85	19.0	23.59	-	0.02
k	0.06	0.09	1.37	0.19	5.07
t_o	-3.45	-	2.20	0.70	7.70
g	-	-	-	0.19	0.21
SEE	5.36	5.55	5.26	0.49	0.54
r^2	0.93	0.92	0.92	0.79	0.74

Table 3: Parameters of the three parameter VBGF for selected skate species. Values presented were calculated for sexes combined unless otherwise stated. Note: k = growth coefficients and L_∞ = theoretical maximum size estimated by the growth function.

Species	Source	Max L_{obs} (cm)	L_∞ (cm)	k(yr^{-1})	Max age$_{obs}$
Amblyraja radiata	Sulikowski et al. (2005)	103.0 (f) 105.0 (m)	124.0	0.12	16
Bathyraja kincaidii	Perez (2005)	61.0 (both)	56.0	0.21	18
Bathyraja trachura	Current study	86.5 (f) 91.0 (m)	112.11	0.06	20
Leucoraja ocellata	Sulikowski et al. (2003)	94.0 (f) 93.2 (m)	131.4	0.06	19
Raja clavata	Brander & Palmer (1985)	-	105.0	0.045	10
Raja erinacea	Waring (1984)	54.0 (both)	52.7	0.35	8
Raja montagui	Ryland & Ajayi (1984)	70 (f) 67 (m)	97.8	0.152	7
Raja microocellata	Ryland & Ajayi (1984)	87.5 (both)	137.0	0.086	9
Raja rhina	McFarlane & King (2006)	124.6 (f) 122.0 (m)	133.8	0.07	26

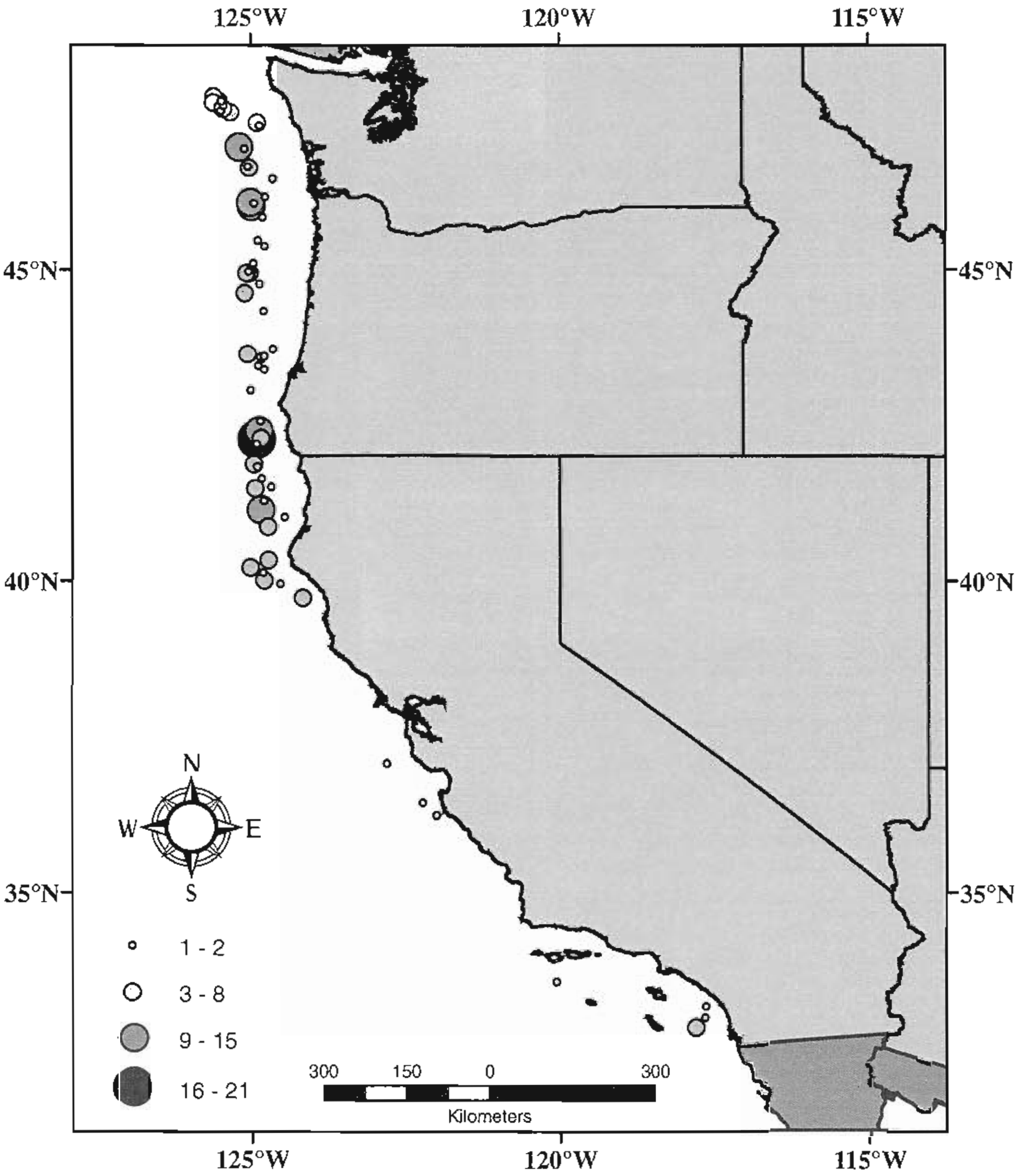

Figure 1: Map of study area indicating distribution of trawl stations from commercial vessels via the NWFSC and Westcoast Groundfish Observers (*n* = 231). Size of points represents the number of specimen obtained per haul.

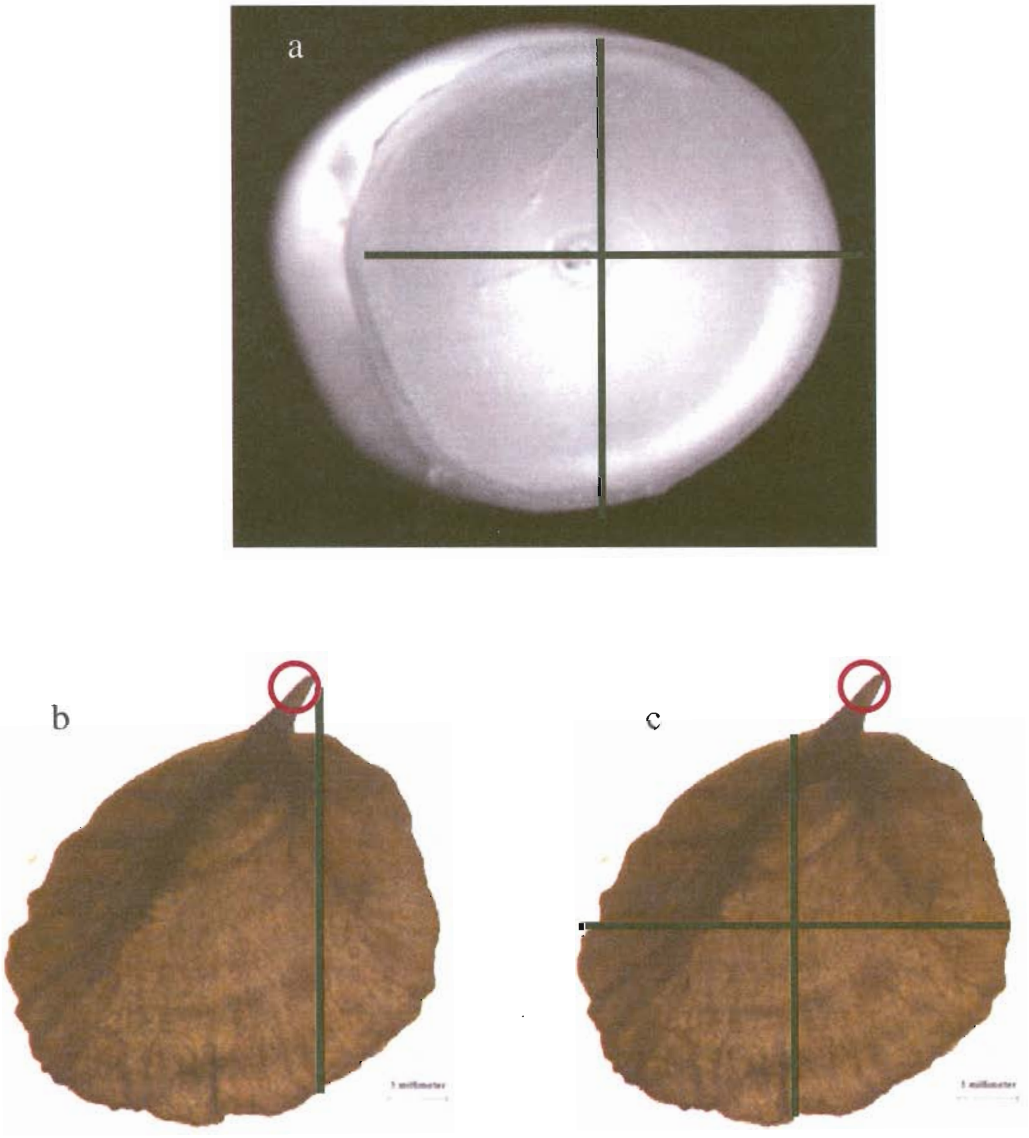

Figure 2: Diagram of structural measurements a) the two perpendicular axes across which the centrum diameter of whole vertebrae were measured. b) The caudal thorn height was measured from protothorn tip (red circles) to thorn base; and c) caudal thorn base diameter was measured across two perpendicular axes.

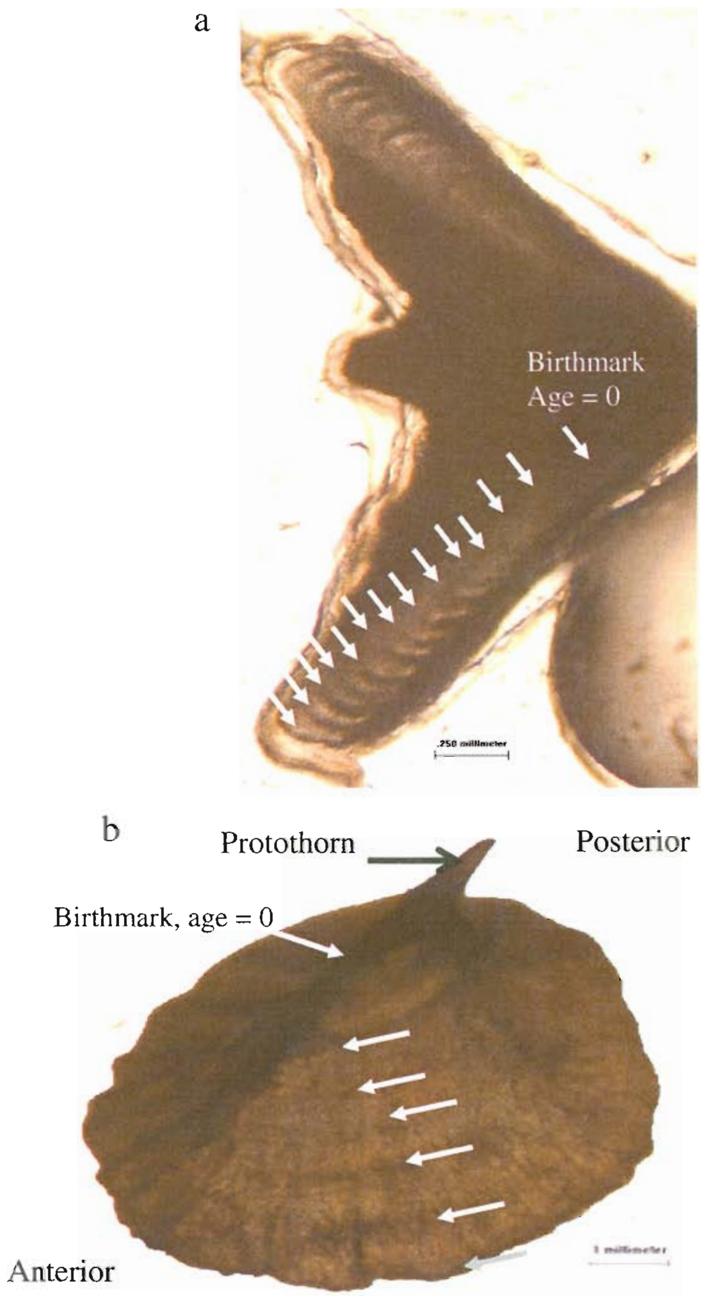

Figure 3: Description of banding pattern for vertebral thin sections from a 59.8 cm TL female (a) and caudal thorns from a 46.5 cm TL male (b). On vertebral thin section the change in angle of the corpus calcerum signifies the birthmark (age = 0). On caudal thorns the birthmark is a prominent ridge which encompasses the thorn below the protothorn. Subsequent white arrows identify opaque bands. (vertebral thin section age = 13, magnification = 3.2x; caudal thorn age = 6, magnification = 1.25x)

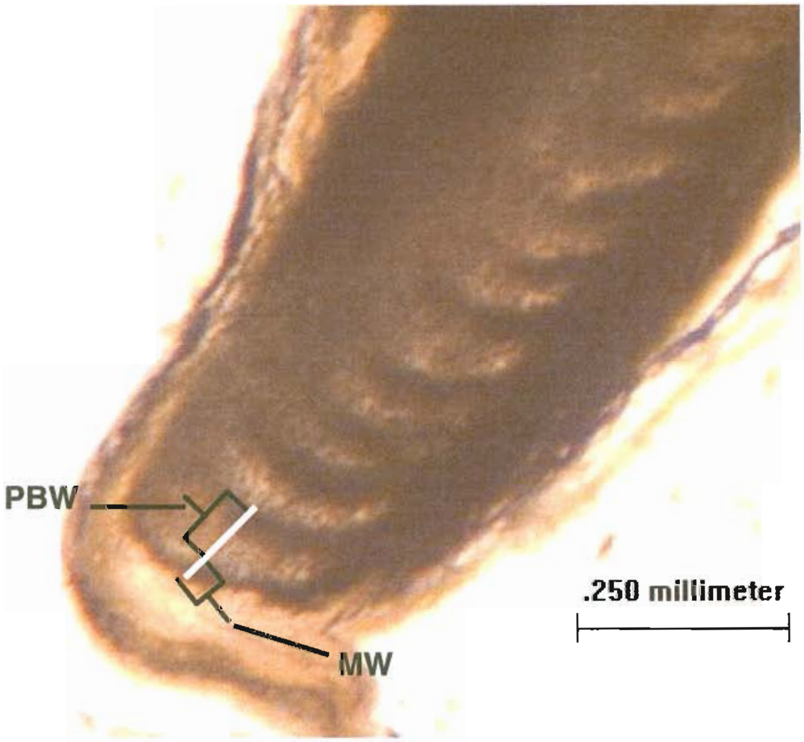

Figure 4: Vertebral thin section edge depicting measurements for Marginal Increment Ratio. Thin section from a 59.8 cm TL female. Note: Margin width (MW) and penultimate band width (PBW), Magnification 3.2x.

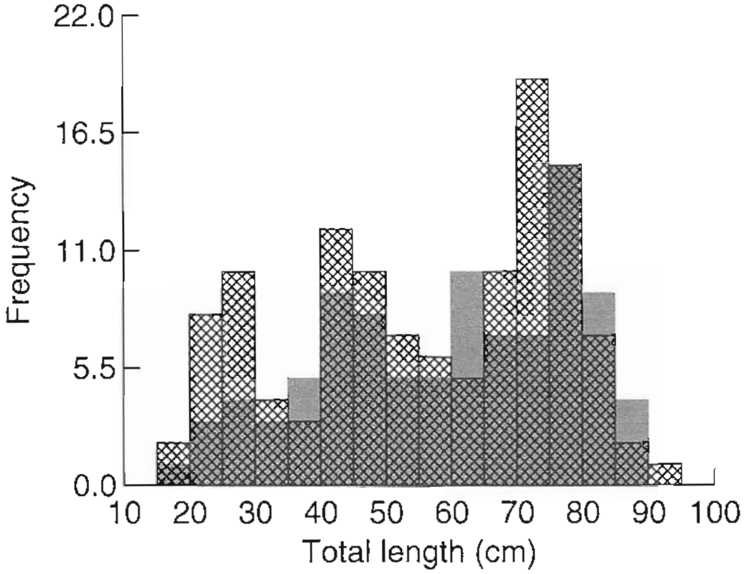

Figure 5: Size frequency histogram of specimens used in age analysis; males (*n* = 102, solid bars) Size frequency histogram of specimens used in age analysis; males (n = 110, solid bars) and females (n = 86, hatched bars).

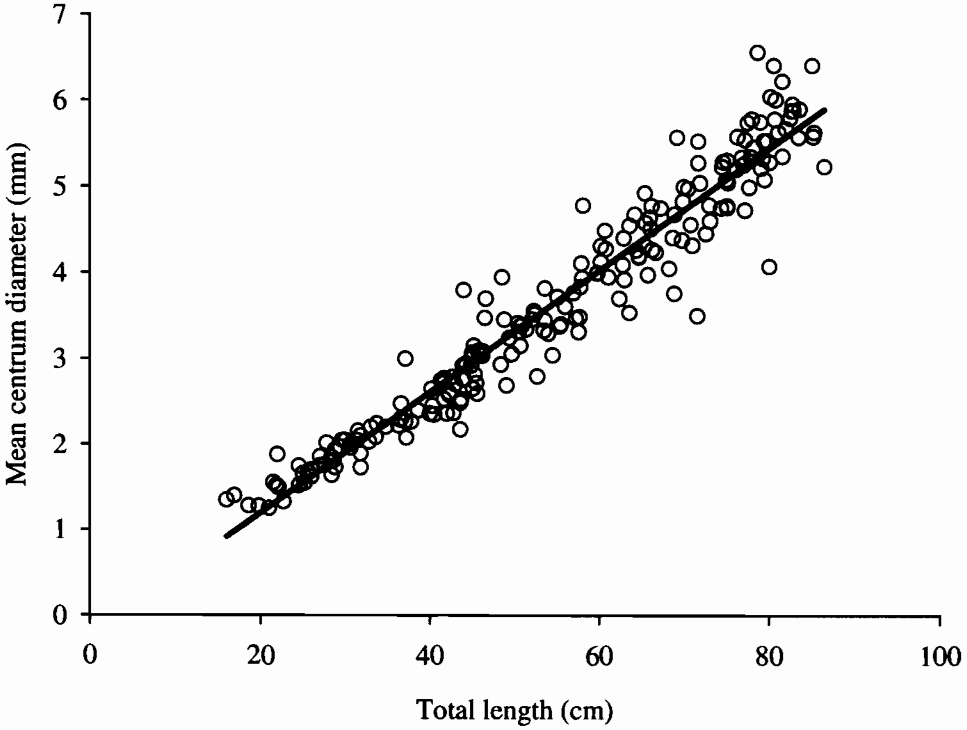

Figure 6: Relationship between mean vertebral centrum diameter and total length for sexes combined ($n = 231$, $y = 0.071x - 0.2402$, $r^2 = 0.92$)

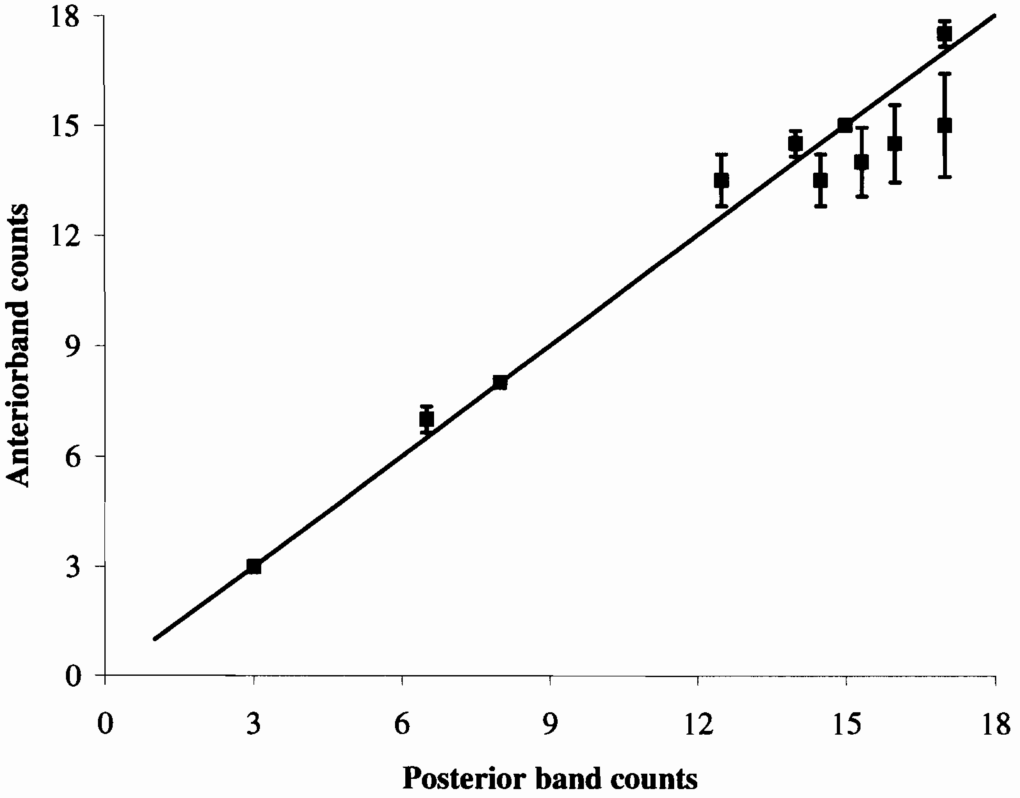

Figure 7: Age bias plot comparing age estimates from the anterior and posterior sections of the vertebral column (*n* = 11). The 45° line represents 1:1 agreement between locations. Error bars are ± standard error.

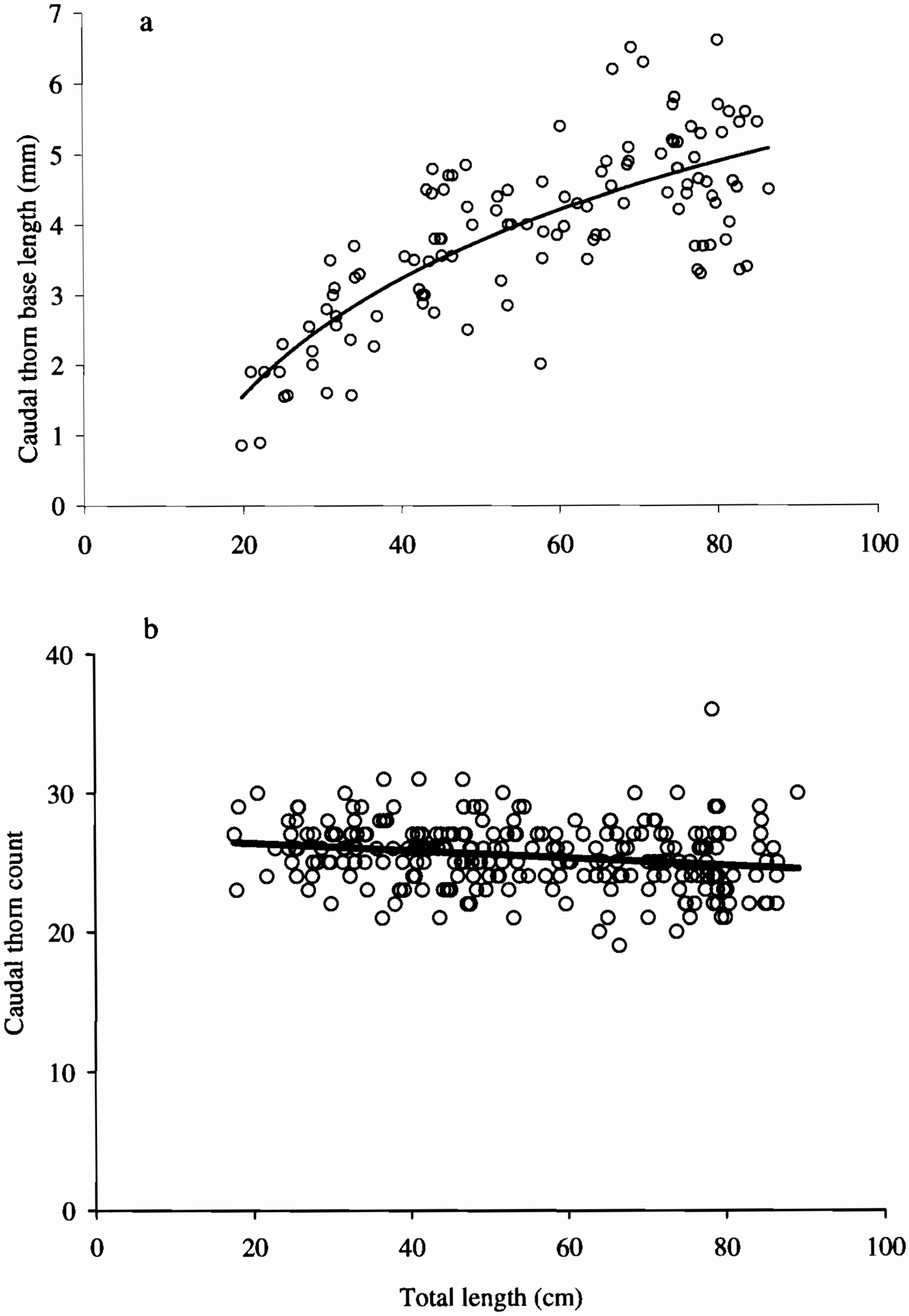

Figure 8: Best fit relationships between caudal thorn base length and somatic growth (a; $y = 2.4073\mathrm{Ln}(x) - 5.652$, $r^2 = 0.60$, $n = 100$) and caudal thorn count and somatic growth (b; $y = -0.0266x + 26.91$, $r^2 = 0.04$, $n = 248$) are depicted for *Bathyraja trachura*.

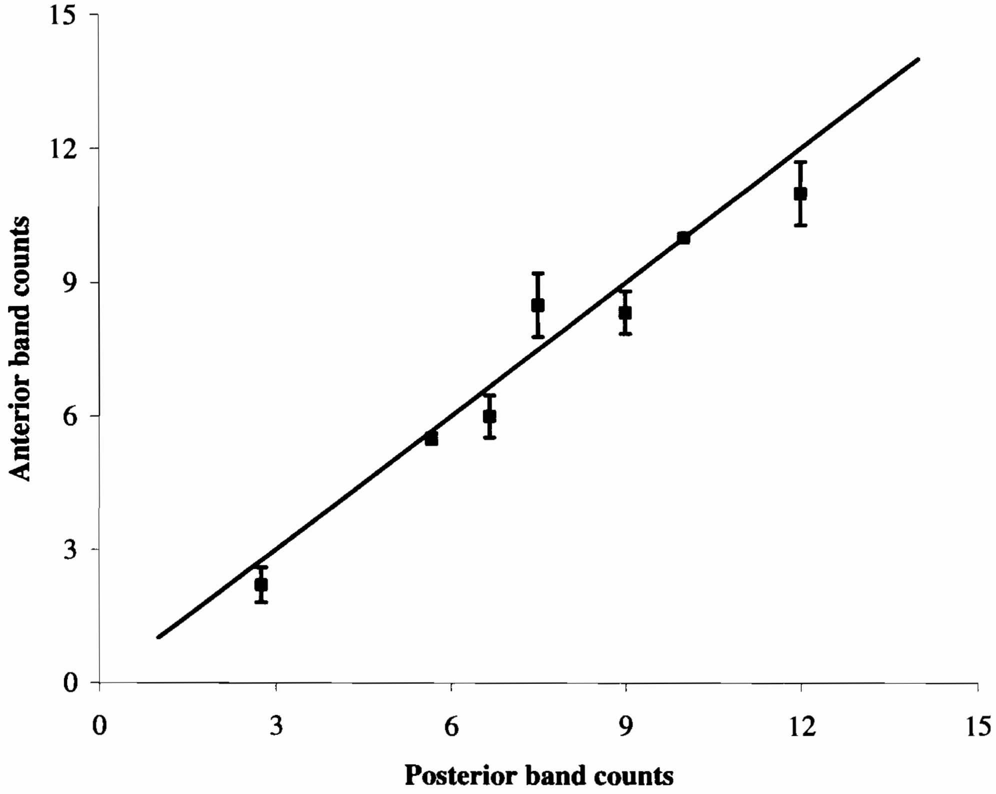

Figure 9: Age bias plots of anterior and posterior age estimates of caudal thorns from seven specimen. 45 ° line represents 1:1 agreement between locations.

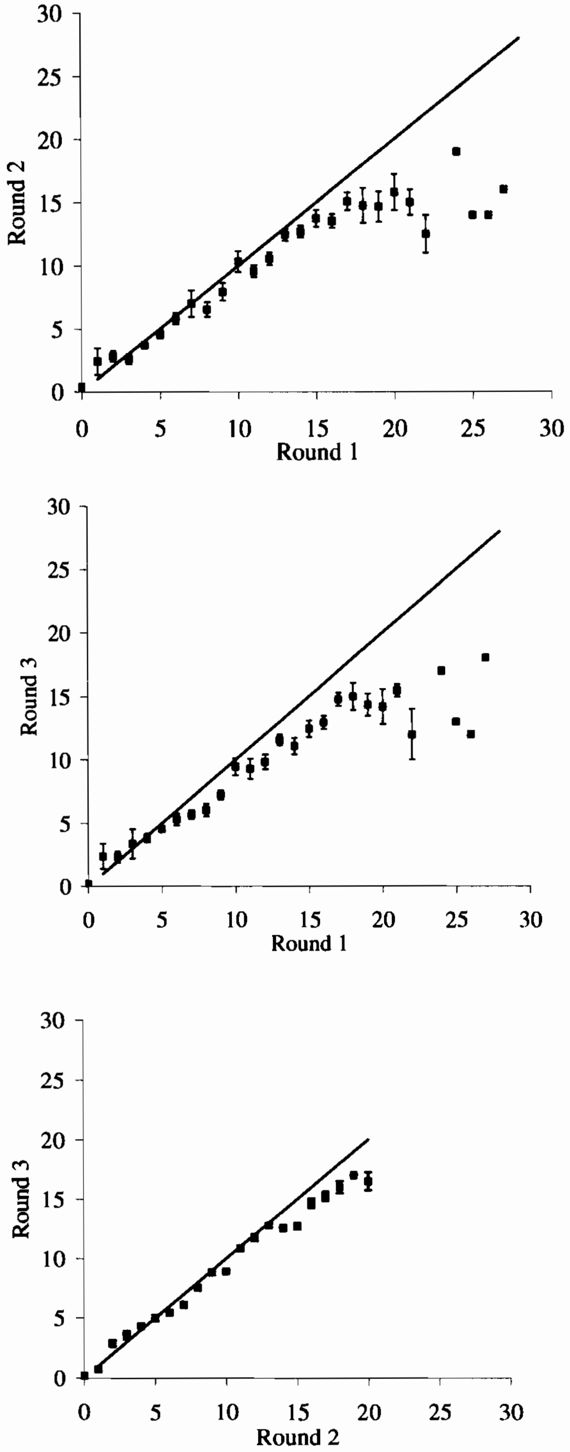

Figure 10: Age bias plots of vertebral thin sections comparing three independent rounds of band counts by one reader (*n* = 197).

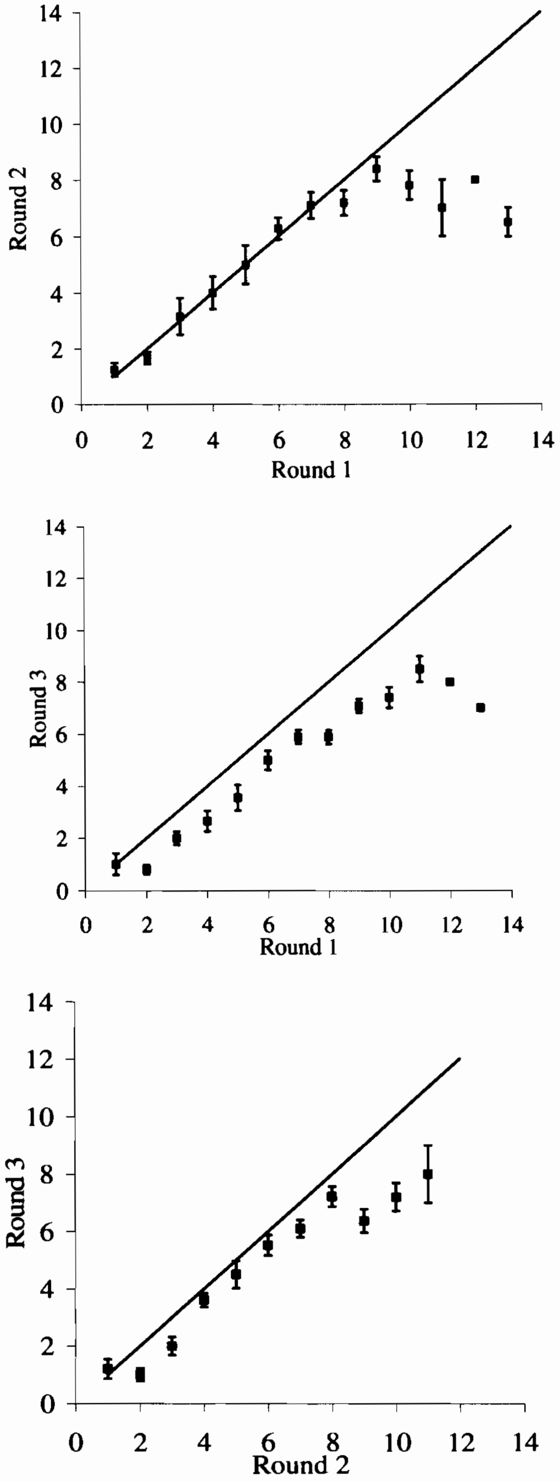

Figure 11: Age bias plots of whole caudal thorns comparing three independent rounds of band counts by one reader (*n* = 96).

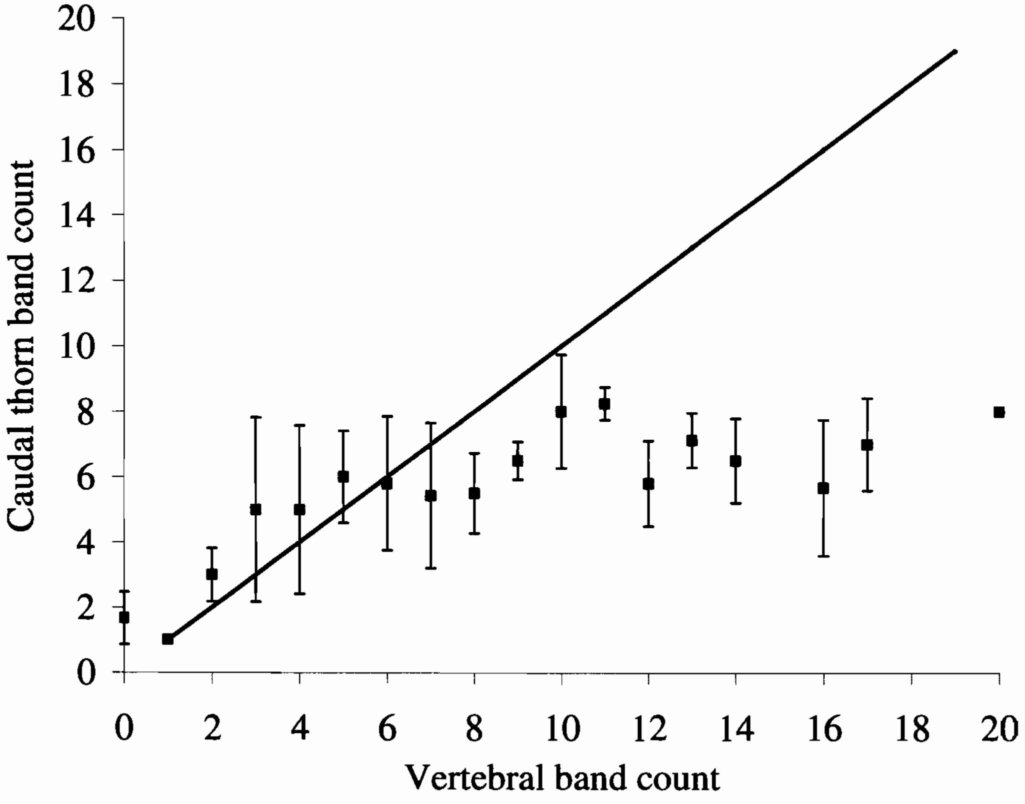

Figure 12: Age bias plot of caudal thorn and vertebral age estimates (*n* = 74). The 45 ° line represents 1:1 agreement of age estimates between structures.

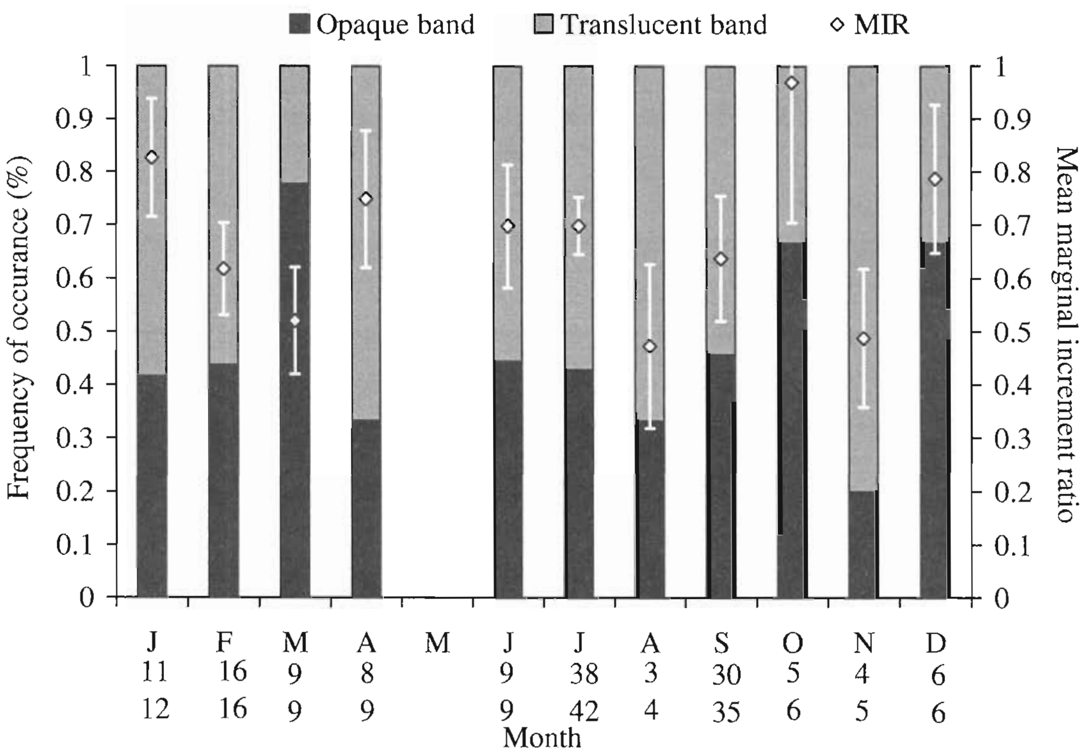

Figure 13: The frequency of occurrence (FO; *n* =153) of opaque and translucent bands and mean Marginal Increment Ratio (MIR; *n* =139) are plotted by month. Black bars indicate frequency of opaque bands, grey bars depict frequency of translucent bands, and white diamonds represent mean MIR values. Numerical values reported below month indicate sample size of MIR (top) and FO (bottom).

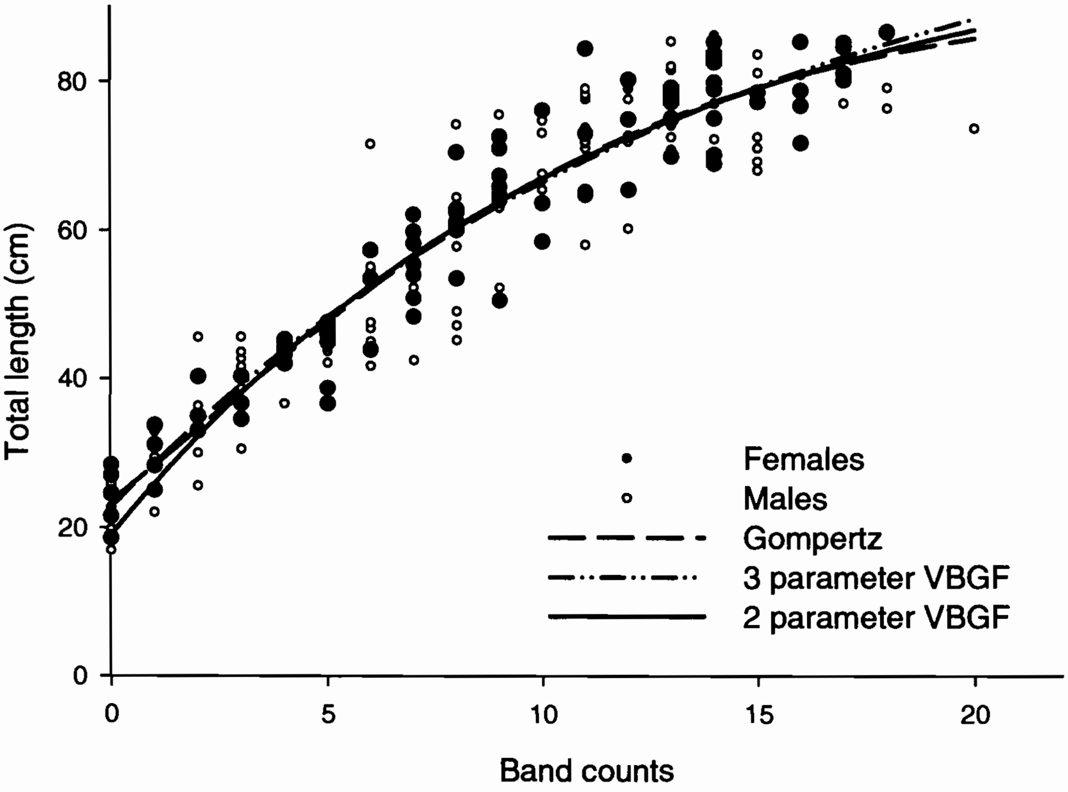

Figure 14: Growth functions fitted to length-at-age data for combined sexes. Note VBGF = von Bertalanffy growth function.

Chapter 3: Reproductive biology of the roughtail skate, *Bathyraja trachura*

INTRODUCTION

Elasmobranch fishes have a diverse array of reproductive modes that can be categorized into two basic groups: oviparity (egg laying) and viviparity (live bearing) (Wourms and Demski 1993, Carrier et al. 2004). All skates exhibit oviparity in which oviducal glands secrete an egg case around a fertilized egg and once completed the egg case is deposited on an object or substrate (Hamlett and Koob 1999). Timing of egg case formation can range from 12 – 24 hours and females can deposit multiple cases over several months. Gestation is species specific and can range from a few months to a year (Hamlett and Koob 1999).

Timing of the reproductive cycle, (e.g. peak periods of gamete production, mating, or seasonality of the reproductive cycle) can be inferred using gonad indices (Hamlett and Koob 1999). The gonosomatic (GSI) and hepatosomatic (HIS) indices change through the year as gamete production ensues and lipid reserves are metabolized. The GSI is a relationship between gonad weight and total weight (Nikolsky 1963). The index assumes there is a linear relationship between gonad weight and body weight that remains constant through all developmental stages and the coefficient of variation for gonad weight is constant (Nikolsky 1963, DeVlaming et al. 1982). The HSI is a ratio of liver weight and total weight. Liver weight typically fluctuates as lipid reserves decrease during the production of gametes. These fluctuations are thought to coincide with inverse fluctuations in GSI. When each index is plotted against month, seasonality of the reproductive cycle can be inferred (Hamlett and Kobb 1999).

Timing of the reproductive cycle is needed to develop accurate life history information that is necessary for the development of fishery management plans. The reproductive strategy of *B. trachura* is unknown and detailed information about reproductive biology and maturity is lacking. To address this knowledge, gap I describe the reproductive anatomy of females and males, determine size and age at first, 50% and 100% maturity, and evaluate seasonal differences in maturity between sexes.

MATERIALS AND METHODS

Sample Collection

Skates were obtained from along the Pacific coast of the contiguous United States between 48.6 ° and 33.35° north latitude (Figure 1). Samples were collected from summer and fall 2003 during the Northwest Fisheries Science Center annual groundfish surveys. Additional samples were collected during winter and spring 2004-2005 from commercial fishery landings via the Pacific States Marine Fisheries Commission - West Coast Groundfish Observer Program.

Sex was determined and biological information was recorded from each specimen. Total length (TL), disc length (DL), and disc width (DW) were measured to the nearest 0.1 mm following Hubbs and Ishiyama (1968) and total weight (kg), gonad weight (g), and liver weight (g) were recorded. A size frequency histogram was plotted, for females and males, to determine if the population was sampled adequately. A t-test was conducted to determine if there was a statistical difference between samples sizes of females and males (Zar 1999).

Total length was plotted against TW and DW to determine length-weight and disc length-width relationships. Total length was related to TW using the power equation calculated as:

$$W = aL^b$$

where a is the y intercept and b is the x-intercept (Richards et al. 1963). Following a Cochrans test for equal variance, an ANOVA was calculated to determine if observed length-weight and disc width-length relationships differed significantly between females and males (Zar 1999).

Maturity assessment

Gonad and liver weight were recorded for each specimen and used to identify reproductive development as it relates to TL. To maintain accuracy of each weight, any punctured or leaking organs were not recorded. Uterus width (mm) and oviducal gland width (mm) were measured for females and inner clasper length (mm) and testis length (mm) were measured for males following Hubbs and Ishiyama (1968)..

Reproductive stages were characterized using the maturity levels: 1) embryo; 2) juvenile; 3) adolescent; 4) adult; and 5) gravid, following criteria modified from Walmsley-Hart et al. (1999) by Ebert (2005). Juvenile females were identified by unvascularized ovarian tissue and an oviducal gland that was undifferentiated from the uterus. Adolescent females possessed developing small, white ova, a thickening uterus and an oviducal gland that was beginning to differentiate from the uterus. Adult females had yellow ova, a fully differentiated oviducal gland and the walls of the uterus were thick. Gravid females contained developing egg cases (Walmsley-Hart et al. 1999).

Juvenile males were identified by undifferentiated testes, and small soft claspers that did not extend past the end of the pelvic fins. Adolescent males had highly vascularized testes, claspers that extended beyond the lower lobe of the pelvic fin, but the claspers were weakly calcified. Adult males had fully developed testes and claspers had well calcified terminal cartilage elements (Walmsley-Heart et al. 1999).

Clasper morphology

Clasper morphology is a useful tool for taxonomic differentiation of species (Ishiyama 1958, Ishihara and Ishiyama 1985). The clasper morphology of *B. trachura* was originally described by Ishihara and Ishiyama (1985) from specimens at the northern end of their range (the Gulf of Alaska and Aleutian islands). Additionally, Craig (1993) described the clasper morphology and several additional morphological traits of *B. trachura* from specimens in the Bering Sea and adjacent waters. Using specimens from the southern end of their range, I described and compared clasper morphology. Clasper terminology (dorsal terminal 1, dorsal terminal 2, dorsal terminal 3, accessory terminal, ventral terminal, axial cartilage, pseudosiphon) followed Leigh-Sharp (1924) and Ishiyama (1958).

Age and size at maturity

Age and size at maturity was determined using a logistic model. The sampled population was separated into discrete 15 cm TL size intervals and the proportion of mature to immature individuals within each interval was determined. The logistic curve was fitted using the graphical program SigmaPlot version 8.0 (SPSS Inc., 2002) calculated as:

$$Y = (1 + e^{-(a+bX)})^{-1}$$

the inflection point of the curve represented the median number at which 50% of the individuals within the sampled population were mature (Roa et al. 1999). The asympote was the size that 100% of the individuals within the sampled population were estimated to be mature.

Size at maturity was evaluated secondarily by comparing oviducal gland width (females) and inner clasper length (males) to TL. The onset of maturity was determined graphically and was signaled by the sudden increase in size of the oviducal gland and inner clasper. The relationship of these organs with TL was used to help secondarily verify the onset of maturity.

Seasonality of the reproductive cycle

To identify potential seasonality of the reproductive cycle, GSI and HSI indices were calculated. The GSI incorporates gonad mass as a percent of total mass and was calculated as:

$$GSI = (g/b) * 100$$

where g is total gonad mass and b is total body mass (Nikolsky 1963). The HSI was calculated by relating liver mass to total body mass:

$$\mathrm{HSI} = (h/b) * 100$$

where h is liver mass and b is total body mass (Braccini and Chiaramonte 2002). The GSI and HSI values were graphed against month (± standard error) to evaluate seasonality of the reproductive cycle. Following a Cochrans test for equal variance, an ANOVA was used to identify significant differences in GSI and HSI calculations between sexes and among months (Zar 1999).

Seasonality of the reproductive cycle also was evaluated by comparing mean ovum diameter to season. The largest ovum in either ovary were measured for all mature females and a monthly mean was calculated. These values (± standard error) were plotted by month and used as a secondary examination of reproductive seasonality.

RESULTS

Sample collection

In total, 478 samples (214 females, 264 males) were obtained from June 2003 through May 2005. The size distribution for both sexes encompassed the complete size range reported for this species. Females ranged in size from 14.5 to 86.5 cm TL and males ranged in size from 16.0 to 91.0 cm TL. Both sexes showed a bimodal size distribution and peak abundance occurred at 40-50 cm and 75-80 cm TL (Figure 2).

Disc width-length ($p = 0.329$) and weight-length ($p = 0.412$) relationships were not statistically different between sexes; therefore, data were combined. There was a positive linear correlation between DW and TL ($y = 0.6152x + 1.6713$, $r^2 = 0.99$, $p < 0.01$) (Figure 3). A significant curvilinear relationship exists between TL and total weight (($y = 2E\text{-}06x^{3.287}$, $r^2 = 0.97$, $p < 0.01$) (Figure 4).

Maturity assessment

Bathyraja trachura contained paired functional oviducal glands that appeared to develop egg cases simultaneously. Mature females had yellow vitellogenic oocytes in the ovaries, the mean largest ovum diameter was 25.7 mm (± 1.5) (Figure 5a,b). In adults, the oviducal glands formed a distinct heart shape and were completely differentiated from the uterus; mean oviducal gland width was 46.6 mm (± 1.4). Adolescent females had white non-vitellogenic oocytes <1 cm that were developing in each ovary. The oviducal gland in maturing females was beginning to form a bean-shape with a mean diameter width of 27.1 (± 1.8) mm and was not clearly differentiated from the uterus (Figure 5c,d,e).

Mature male specimens contained well-developed testes ranging from 66.2 to 198 mm in length (Figure 5a). Immature and maturing individuals contained developing testes that appeared as an opaque mass becoming increasingly vascularized (Figure 5b,c,d). Adolescent testis length ranged from 41.0 to 60.0 mm and juvenile testis length ranged from 9.0 to 49.0 mm.

Clasper morphology

The claspers of two adult males and two adolescent males were examined. As male *B. trachura* began to mature, noticeable changes in calcification of the clasper were apparent. During maturity stage three, there was a broad range of calcification within the clasper. In mature males the clasper was broad with a slight distal taper and smooth with white mottling on the tips. Each consisted of one accessory terminal, axial cartilage, three dorsal terminals, ventral margin and ventral terminal. The dorsal terminal (dT1) was broad, curving from dorsal around to ventral side where it connected with ventral terminal (vT) to form the pseudosiphon (ps1) (Figure 7a). dT1 covered the dorsal side of all elements. The axial (Ax) extended past vT, and distal edge overlaped dorsal terminal (dT3). dT3 was long, connected with dT1 along lateral-posterior margin. The ventral margin (vM) was pointed forming an external projection (Figure 7b). The accessory terminal 1 (aT1) was long, attached anterior attachment at distal edge of vM, lateral-posterior attachment with Ax.

Age and size at maturity

At the onset of female maturity (~73 cm TL), there was an abrupt change in the development of the oviducal gland with regard to TL. Oviducal gland width for juvenile and adolescent females ranged between 1.0% and 3.8% of TL. Oviducal gland width for adult and gravid females was between 6.0% and 6.2% of TL. This increase identified the transition of individuals from immature into mature adults (Figure 8).

Size at 50% female maturity was estimated at 72 cm TL (Figure 9a) equaling 86% of their asymptotic length. The smallest mature female was 70.1 cm TL (14 yrs) and all females > 78.0 cm TL were mature. The largest immature female was 78.1 cm TL (13 yrs). Age at 50% maturity was estimated at 14 yrs (Figure 9b).

At the onset of male maturity, (~66.0 cm TL) there was an abrupt change in the development of the clasper with regard to TL. This change identified the transition of individuals from juveniles into adults (Figure 10). Inner clasper length, as a percentage of their mean asymptotic length, was 0.5% for juveniles, 14.0% for adolescents and 23.9% for adults. All males shorter than 65.0 cm TL were juveniles and had a mean inner clasper length of 22.6 mm ± 10.6.

Size at 50% male maturity, as indicated by the logistic curve, was estimated at 77.0 cm TL (Figure 9a) at 77% of their asymptotic length. First maturity occurred at 66.0 cm TL and all males were mature by 81.0 cm TL. The longest immature male was 66.7 cm TL (10 yrs) and the shortest mature male was 66.0 cm TL (11 yrs). Age at 50% maturity occurs at 13 yrs (Figure 9b).

Seasonality of the reproductive cycle

GSI and HSI values did not support a seasonal trend in the female reproductive cycle. Fifty-five percent of the samples were discarded because of deterioration of the ova. Damaged gonads were not weighed, therefore only 16 samples were intact and used for GSI calculation. Average GSI of skates was not statistically different throughout the year ($F_{0.05,9,6} = 0.411$, $p = 0.855$), indicating that there was no significant change in ovum weight among months (Figure 11a).

The female liver did not decompose while defrosting; none of the samples were discarded. Although the lowest mean HSI value occurred in September, values did not significantly change during the year ($F_{0.05,9,103} = 0.197$, $p = 0.993$) (Figure 11b). No mature females were captured in June.

Largest ovum diameter increased from July through October indicating that peak ovum diameter occurred during winter (Figure 12). Of the 47 mature females sampled, decomposition of ova during defrosting decreased sample size. Ovum diameter was measured from a total of 37 individuals. Mean ovum diameter was greatest in October (25.1 cm) and lowest in January (11 cm). Samples were unavailable for March, April, June and November.

Seasonal trends of the male reproductive cycle were not evident using GSI and HSI indices. In total, 92 mature males were collected, and 68.5% of the samples were discarded. Damaged organs were not weighed, therefore only 63 samples were intact and used for GSI calculation. There was a noticeable drop of GSI values in July but average male GSI was not statistically different throughout the year ($F_{0.05,11,58} = 1.95$, $p = 1.150$), indicating that there was no seasonality of the reproductive cycle (Figure 9a).

The male liver did not decompose while defrosting, providing more samples. Fewer than 1.0 % of the samples were discarded. There was a noticeable drop of male HSI values (corresponding with a drop in GSI values) in July however, this was not significant ($F_{0.05,11,51}$ = 0.753, p = 0.684) (Figure 9b). HSI values were similar throughout the year.

DISCUSSION

Sample collection

Low sample size of adult females affected the ability of this study to define the female reproductive cycle for *B. trachura*. One factor that decreased sample size was the inability to sample below a depth of 1,200 m during trawl surveys. Samples were obtained from commercial fisheries and fishery-independent surveys, but neither source used trawling gear that could fish through the entire depth range of this species. Therefore, it is possible that the largest specimens were not captured.

Additionally, processing of frozen rather than fresh samples caused degradation of reproductive organs. Ova and testes of juvenile specimen were not weighed or measured in most cases because they decomposed while defrosting. While mature specimens maintained structure longer during defrosting, this did not improve sample size. Future work on fresh specimens is needed to obtain a clear understanding of the reproductive cycle for this species.

Clasper morphology

Ishihara and Ishiyama (1985) originally described the clasper morphology of *B. trachura* from a specimen located north of the Aleutian Islands (54° 20N 166° 55W). The clasper morphology of the specimens examined in the current study were consistent with the original description suggesting that the population of *B. trachura* in the ENP (48.6° latitude and 33.35° latitude) is similar in clasper morphology to those north of the Aleutian Islands. However, Craig (1993) also examined males from the same region as Ishihara and Ishiyama (1985) and suggested there were three morphotypes. Morphotypes A and B both lack a pseudosiphon and morph C has a pseudosiphon. A pseudosiphon was present on the males (n=2) examined in the current study and on the one specimen examined by Ishihara and Ishiyama (1985). However, the other morphological characteristics for morphotype C as cited by Craig (1993) are not consistent with *B. trachura* specimen examined in the current study. It is inconclusive if the morphotypes A, B, or C occur south of the Gulf of Alaska, or if additional morphotypes exist for this southern population. The holotype of *B. trachura* was taken off southern California within the survey area of the current study.

Age and size at maturity

Skates have a life history of late age at maturity and slow growth with females maturing slower and later than males (Abdel-Aziz 1992, Smale and Compagno 1997, Ebert 2005, Gedamke et al. 2005, Licandeo et al. 2006). Age at maturity was attained by *B. trachura* at 14 yrs (females) and 13 yrs (males). Females matured at a larger size and later age than males however this relationship was not statistically significant. *Bathyraja trachura* also reached 50% maturity at 85% (females) and 77% (males) of their asymptotic length. Ebert (2005) also estimated size at maturity from *B. trachura* samples captured in the eastern Bering Sea. He found that 50% maturity was achieved at 73.5 cm

TL females and 75.5 cm TL males. These lengths are similar to what was determined in the current study for *B. trachura* specimen in the ENP (72 cm TL females and 77cm TL males). However, (Ebert 2005) also expressed low sample size and an incomplete size range which might account for any discrepancy between these studies. Further work is needed to determine if the populations are connected.

Seasonality of the reproductive cycle

Seasonal fluctuation of female GSI and HSI were not significant and indicated that female *Bathyraja trachura* did not have a well-defined reproductive cycle. As previously described, low sample size may attribute to the lack of significance between the indices. However, gravid females were obtained from five non-consecutive months of the year (February, March, May, September, and December) suggesting that females were capable of depositing egg cases year round.

The patterns exhibited by GSI and HSI for *B. trachura* contradict traditional theory of an inverse relationship between the organ weights (Nikolsky 1963). The pattern of male GSI and HSI also showed no peak in gamete production. However, in July there was a noticeable drop in GSI which corresponded with a drop in HSI. This drop was not significant and can be attributed to low sample size that month. GSI and HSI indicated that males are capable of year round sperm production. Therefore, hormones such as testosterone and estradiol could be better indicators of seasonal changes in reproductive cycle (Sulikowski et al. 2005a,b).

While the gonad indices show seasonal change in testicular structure, they do not accurately identify mating (Teshima 1981, Maruska et al. 1996, Sulikowski et al. 2005a). Reproductive research using cellular methods (histology), or steroid hormones do not support use of the GSI to determine reproductive readiness (DeVlaming et al.1982, Maruska et al. 1996, Sulikowski et al. 2005a). Maruska et al. (1996) found that for the Atlantic stingray (*Dasyatis sabina*), GSI values peaked in October but concurrent histological analysis found maximum sperm production to occur from July to August when testes were decreasing in size. Research by Sulikowski et al. (2004) on the winter skate (*Leucoraja ocellata)* found weak correlation between GSI or HSI and the reproductive hormones estradiol or testosterone. Similarly Sulikowski et al. (2005b) found weak correlation between GSI or HSI and spermatogenesis for both sexes of *Amblyraja radiata*. This evidence further supports the inability of GSI and HSI to positively identify mating period or mature sperm production and exemplifies the need for cellular research on batoid reproduction. As more studies incorporate steroid hormones into reproductive analysis, especially on year round strategists, a clearer understanding of skate life history will unfold.

Bathyraja trachura was found to be a late maturing species making them susceptible to over exploitation. Sustainable fishing has been found to be dependent on age and size at maturity, accurate reporting of catch and replacement mortality of the target species (Brander 1981). Misidentification of close relatives *(Bathyraja abyssicola)* decreases the ability to interpret species-specific fishing mortality; however, because of their relatively large size and slow growth, *B. trachura* maintains an exploitable size for many years prior to achieving reproductive readiness.

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Table 1: Summary of maturity characteristics for skates including species, author, age and size at first maturity, age and size at 50 % maturity for each species. Data are ordered by female maximum total length. Note: asterisks (*) denote data presented within the associated paper, n = sample size and NA = no information available.

Species	Source	Sex	max TL_{obs}(cm)	n	Age_{first} (yr)	TL_{first} (cm)	$Age_{50\%}$ (yr)	$TL_{50\%}$ (cm)
Bathyraja kincaidii	Perez (2005)	F	61.0	247	4	45.0	7.1	46.7
		M	63.5	259	4	44.6	7.5	49.2
Leucoraja ocellata	Sulikowski et al. (2005b)	F	63.5	132	8-9	~74.0	~11	76.0
	Robins *et al.* (1986)*	M	93.2, 110*	98	10-11	~72.0	11	73.0
Bathyraja trachura	Current study	F	86.5	214	8	70.1	14	72.0
		M	91.0	264	9	66.0	13	77.0
Bathyraja trachura	Ebert (2005)	F	88.5	37	NA	75.0	NA	73.5
	Ishihara and Ishiyama (1985)*	M	82.5, 89.0*	31	NA	75.0	NA	75.5
Raja rhina	Zeiner and Wolf (1993)*	F	124.6	68*, 73	7*	70.0	10	83.0
	McFarlane and King (2005)	M	122.0	65*, 101	7*	50.0	7	65.0
Dipturus chilensis	Licandeo *et al.* (2005)	F	125	519	12	94.0	14.4	106.3
		M	107	412	9	75.0	11.2	86.1
Raja binoculata	Zeiner and Wolf (1993)*	F	203.9	68*, 125	10-12*	60.0	8	90.0
	McFarlane and King (2005)	M	183.6	103*, 117	7-8*	50.0	6	72.0

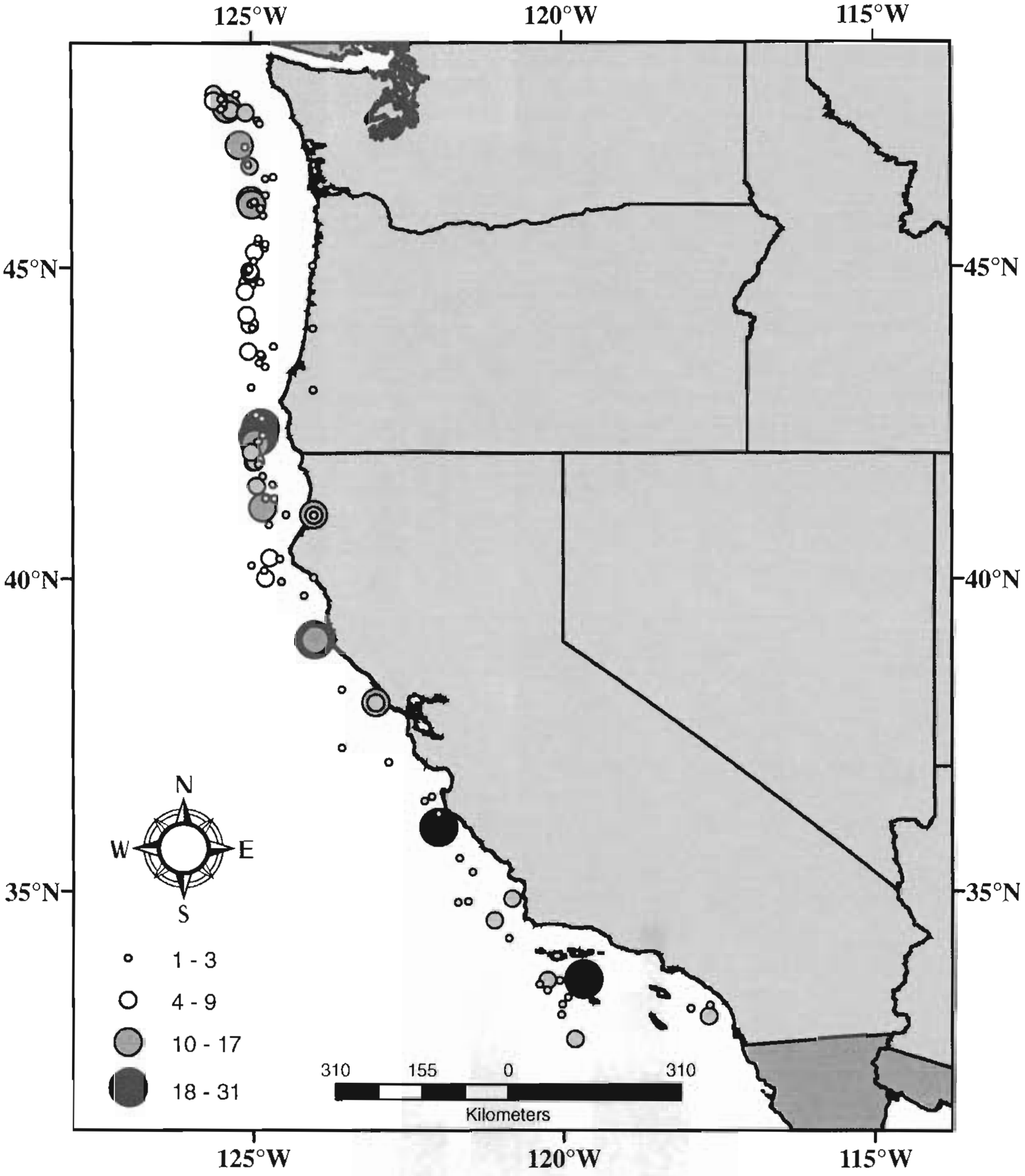

Figure 1: Distribution of samples used in reproductive analysis. Trawl cruises are from commercial vessels via the NWFSC and Westcoast Groundfish Observers (*n* = 478). Size of points represents the number of specimens obtained per haul.

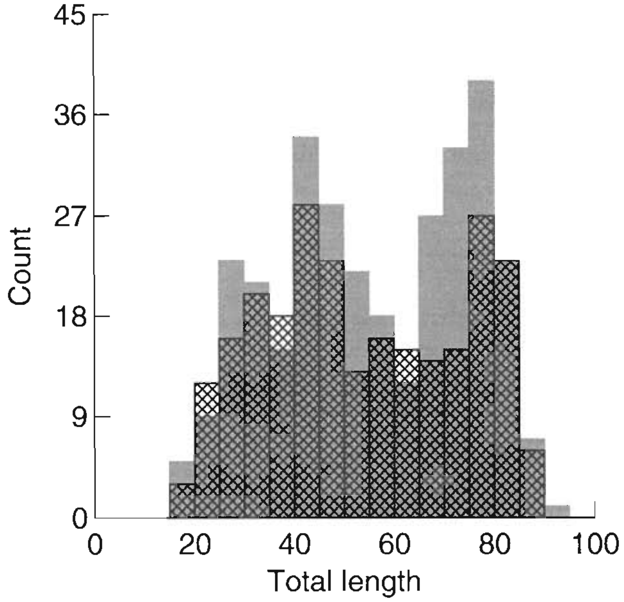

Figure 2: Size frequency histogram used for reproductive analysis of *Bathyraja trachura* females (hatched bars) and males (solid bars).

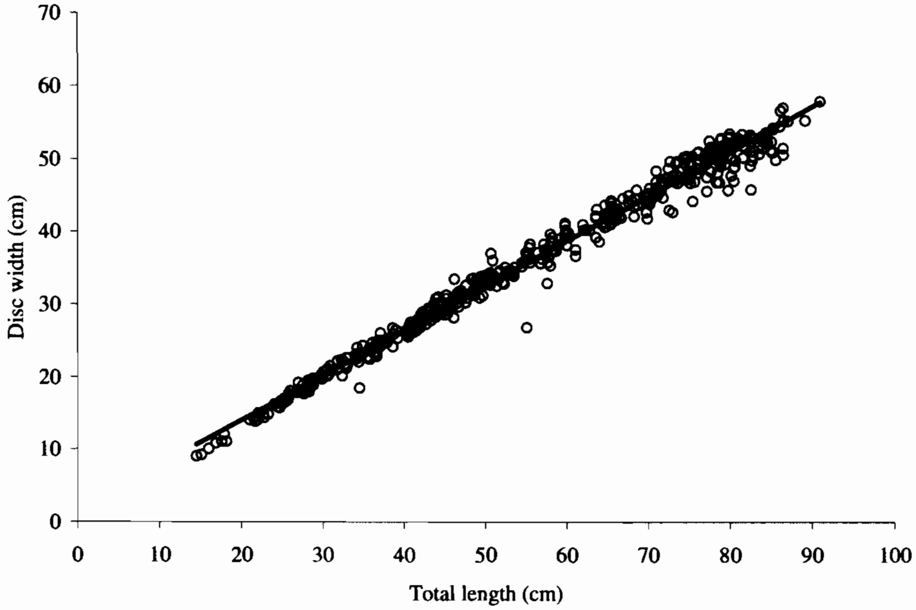

Figure 3: The relationship between disc width and total length for *Bathyraja trachura* (*n* = 478). Both sexes are combined ($y = 0.6152x + 1.6713$, $r^2 = 0.99$).

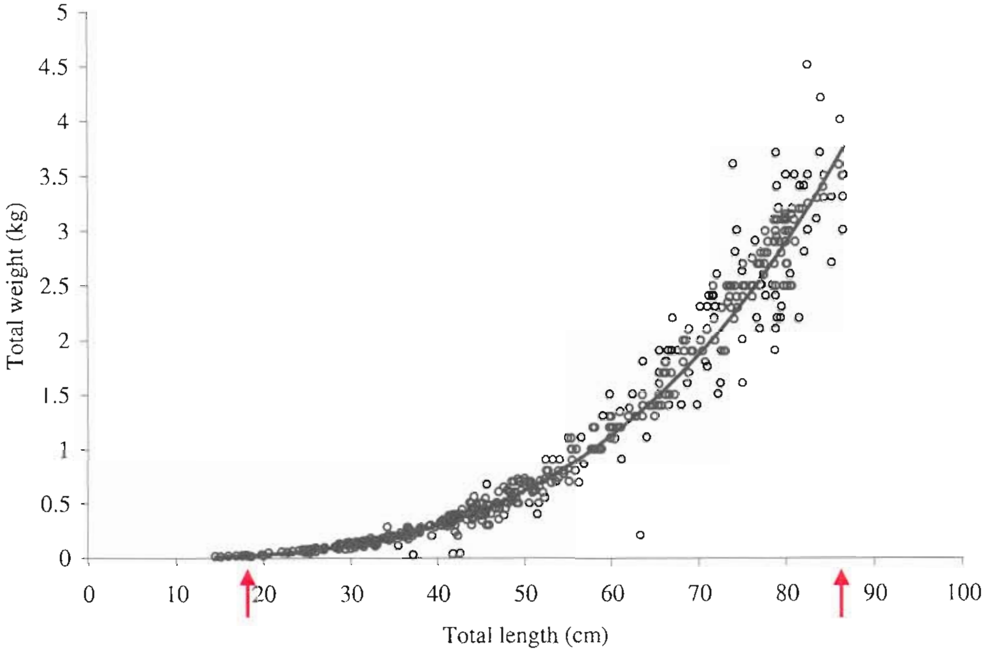

Figure 4: Relationship between total weight and total length (n = 478). Both sexes are combined ($y = 2E\text{-}06x^{3.287}$, $r^2 = 0.97$). Arrows indicate the birth size and maximum reported size as reported by Ishihara and Ishiyama (1985).

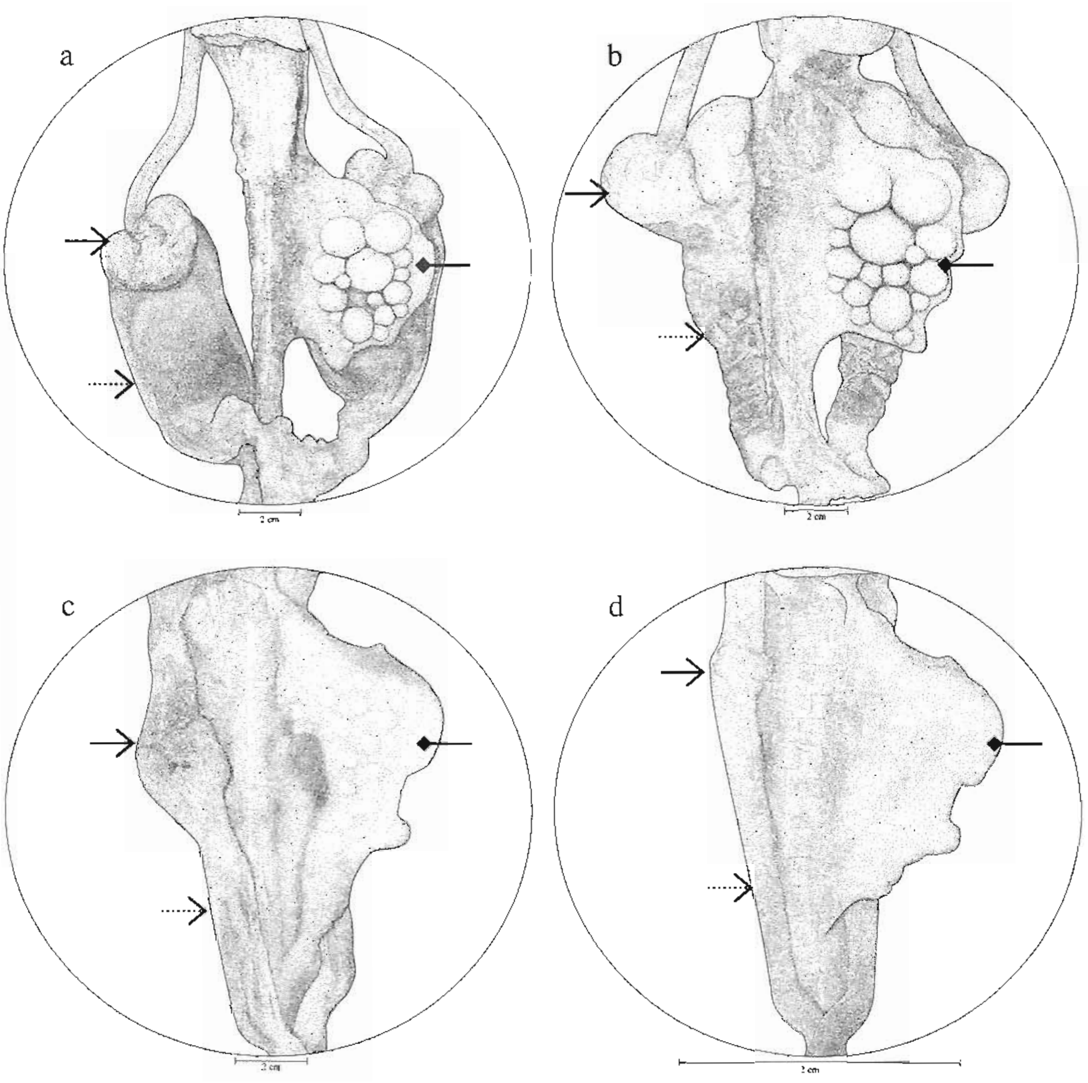

Figure 5: Illustration of female reproductive tract for *Bathyraja trachura:* a) gravid, b) adult, c) adolescent, d) juvenile. Note: oviducal gland (solid arrow), uterus (hatched arrow), ovum (diamond arrow). Illustrated by Laura Dippold.

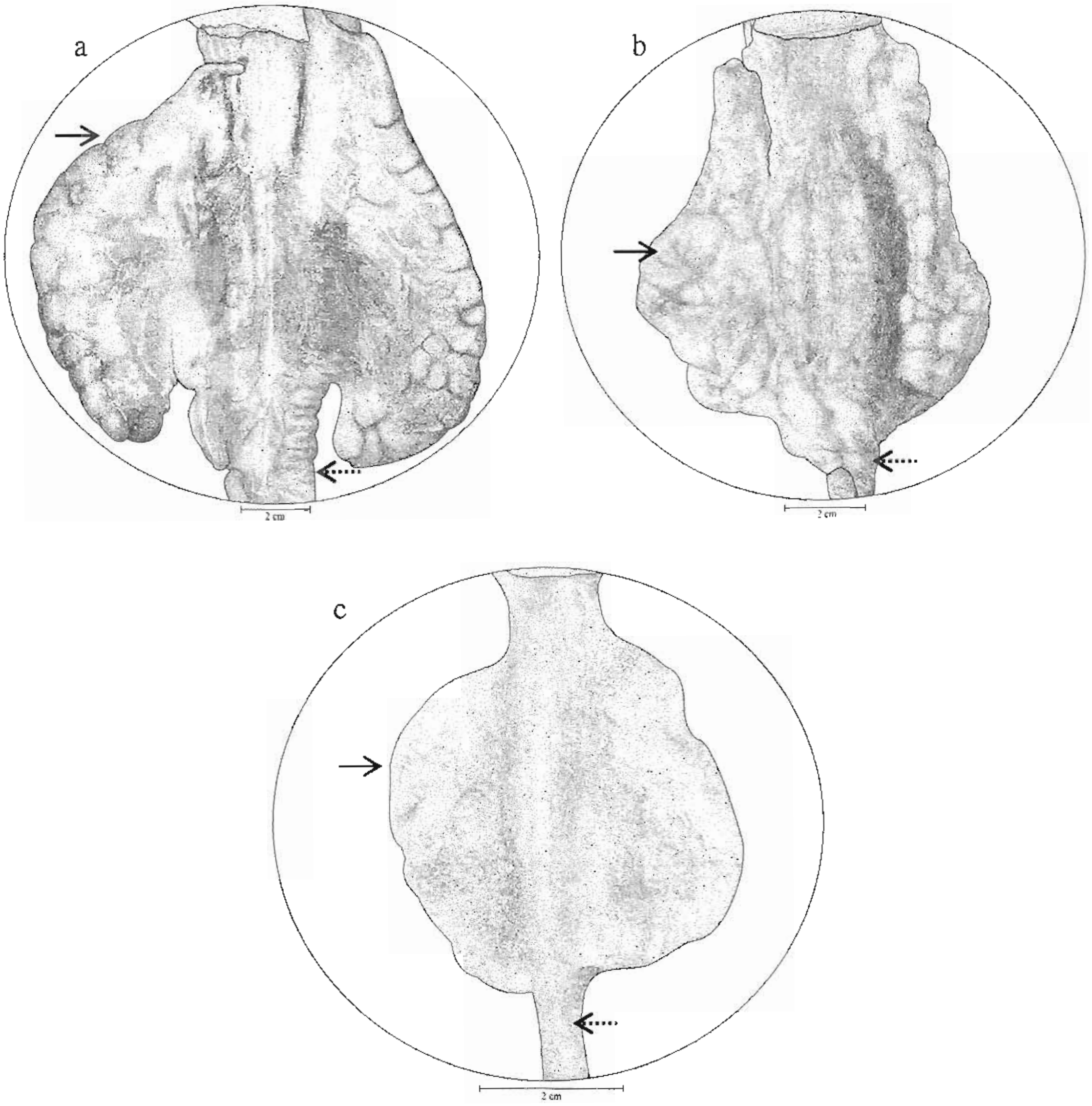

Figure 6: Illustration of male reproductive tract: a) adult, b) adolescent, c) juvenile. Note: testis (solid arrow), epididymis (hatched arrow). Illustrated by Laura Dippold.

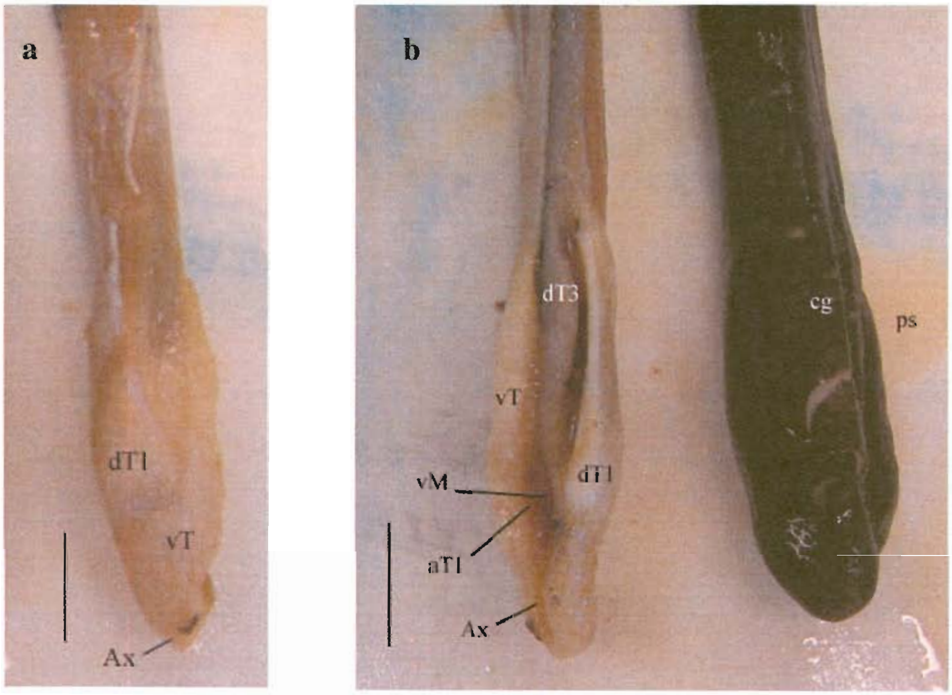

Figure 7: Left clasper of *Bathyraja trachura*. a, ventral view; b, lateral view. aTl, accessory terminal 1; Ax, axial; cg, clasper groove; dT1-dT3, dorsal terminals 1 – 3, ps1, pseudosiphon; vM, ventral marginal; vT, ventral terminal. Scale = 2 cm.

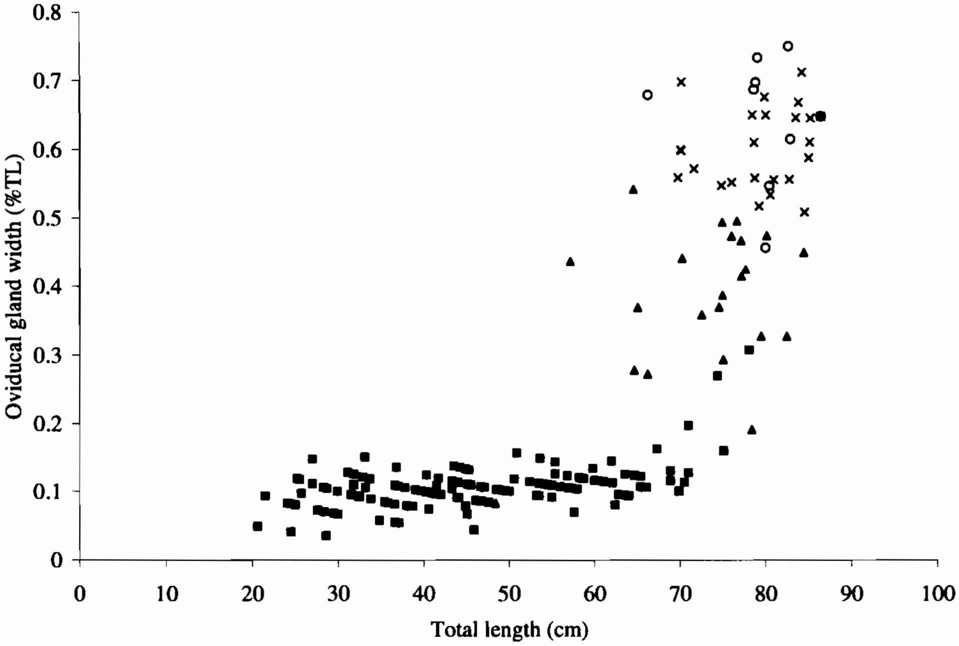

Figure 8: Relationship of total length to oviducal gland width for *Bathyraja trachura* (*n* = 199). Closed squares are juvenile, closed triangles are adolescent, crosses are adult and open circles are gravid females.

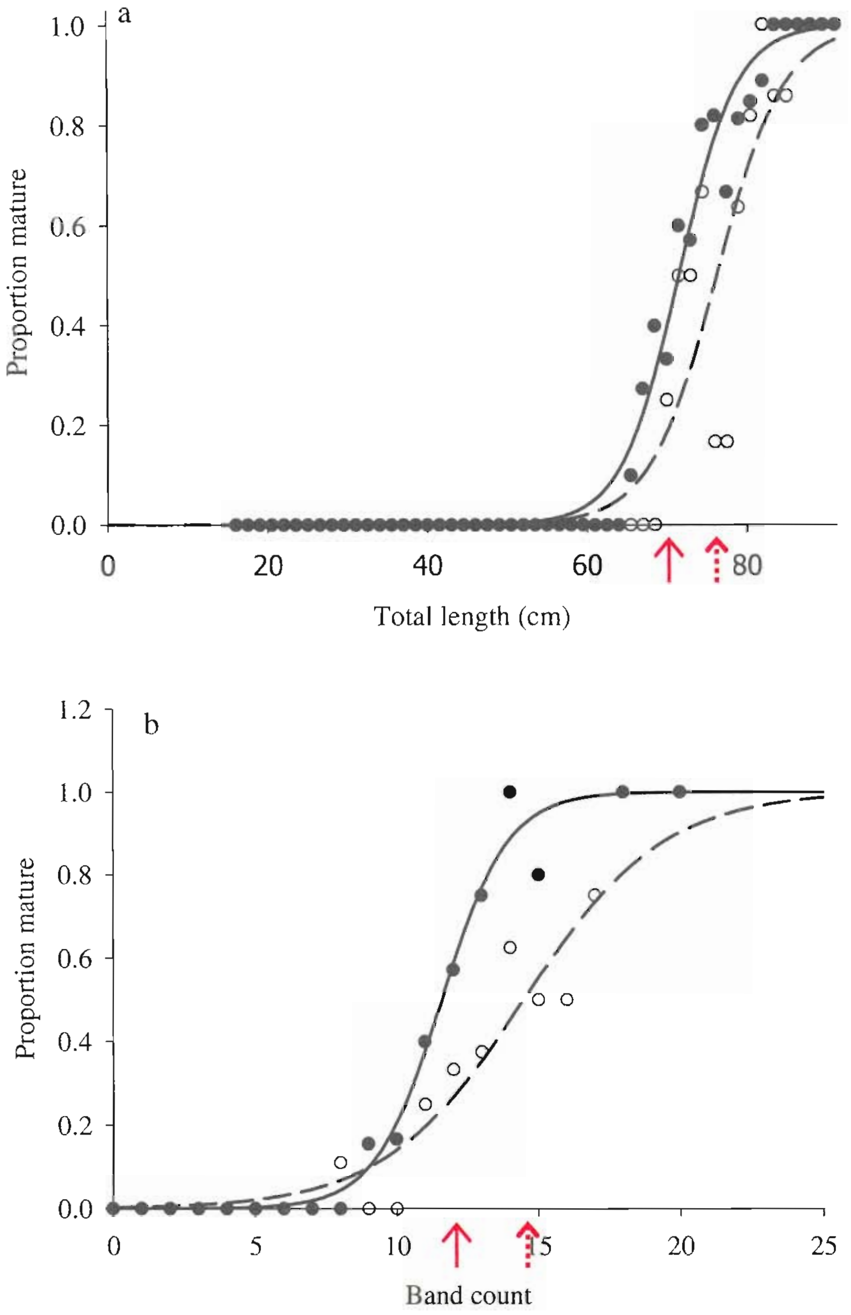

Figure 9: Size at maturity curves (a) and age at maturity curves (b) for females(open circles) and males (closed circles). The arrows indicate age at which 50% of the population is mature for females (broken arrow) and males (solid line).

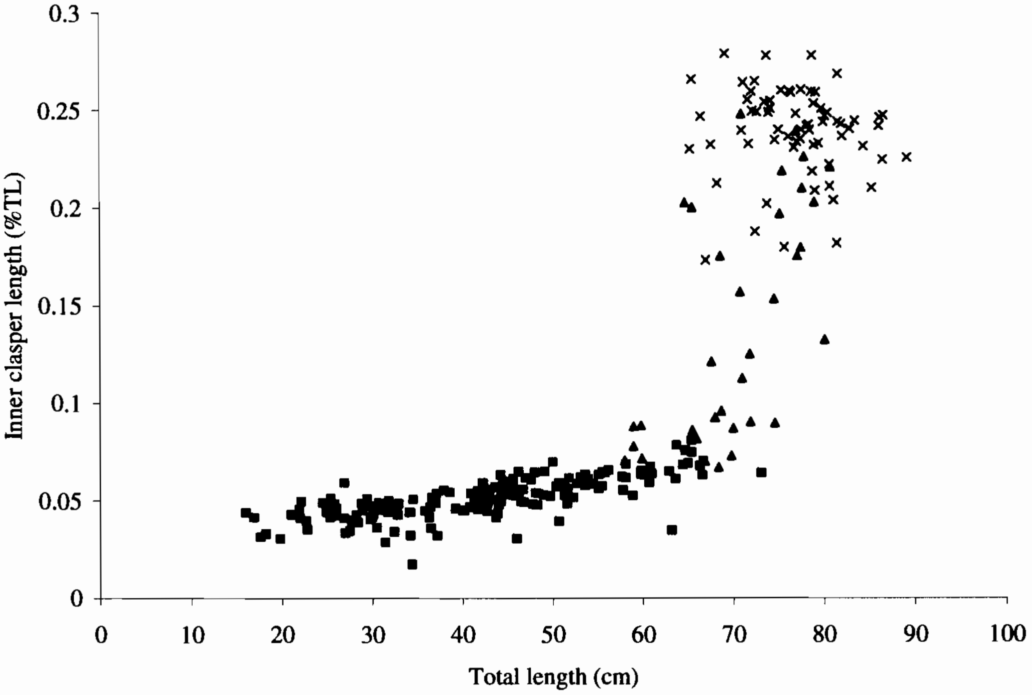

Figure 10: Relationship of total length to inner clasper length for *Bathyraja trachura* (n = 264). Closed squares are juvenile, closed triangles are adolescent, and crosses are adult.

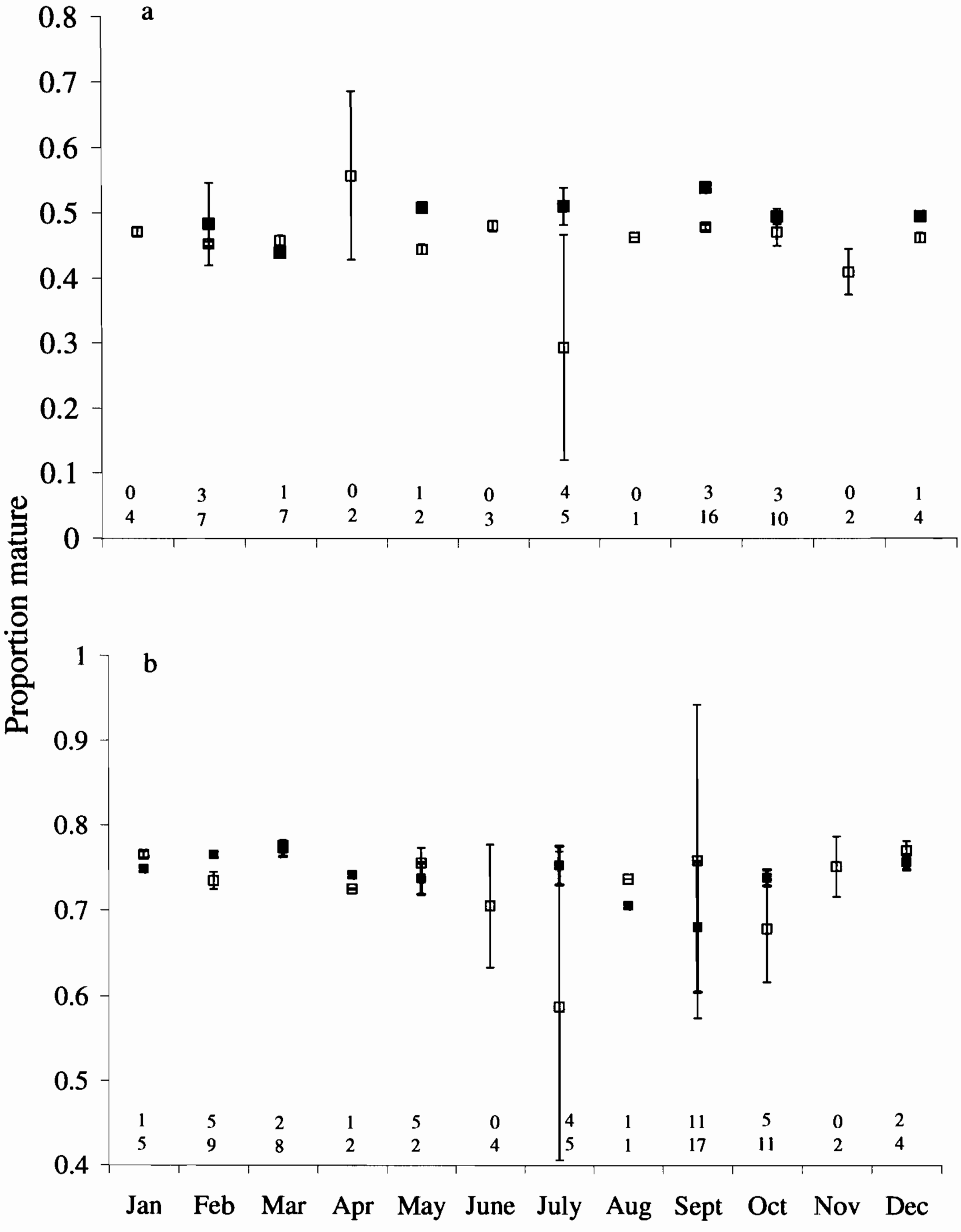

Figure 11: Monthly mean GSI (a) and HSI values (b) for females (solid squares) and males (open squares) ± standard error. Numbers on bottom of graph indicate sample size for females (top) and males (bottom).

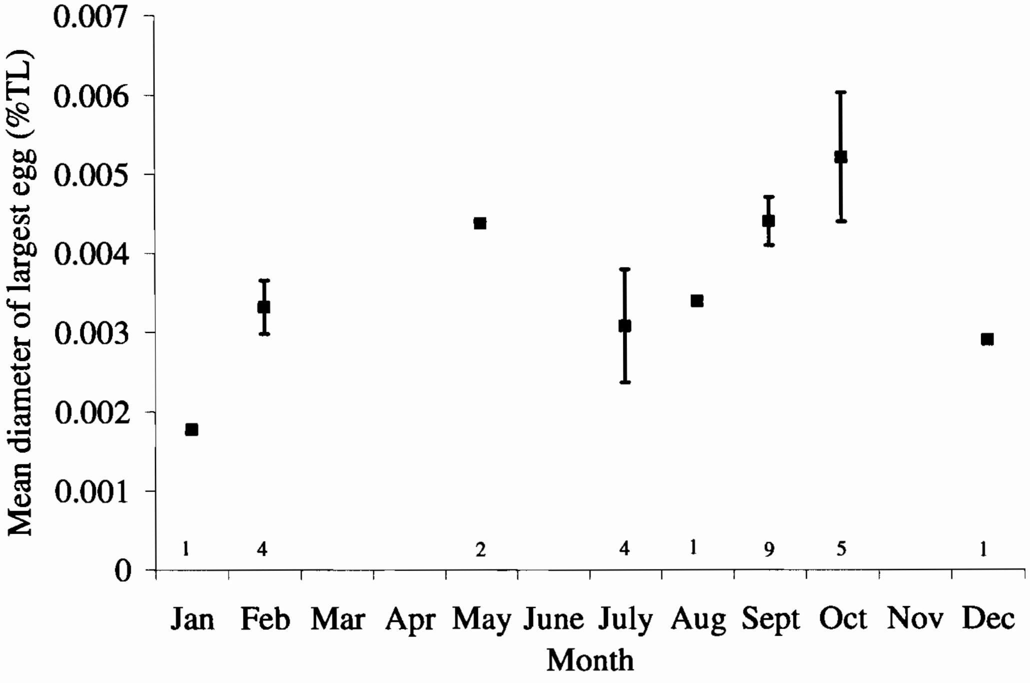

Figure 12: Monthly variation of mean diameter of largest oocyte for female *Bathyraja trachura*. Numbers at the bottom of the graph indicate the quantity of specimen evaluated each month. Error bars are ± standard error.

Chapter 4: Conclusion

FISHERY IMPLICATIONS

As documented in the Atlantic, some skate species are unable to sustain increased fishing pressure (Brander 1981, Walker and Hyslop 1998, Casey and Meyers 1998, Frisk et al. 2002). Skate fisheries in the northwest Atlantic illustrate the effect of fishing pressure on skate populations well. The abundance of skate species in the North Sea was once dominated by the common skate (*Dipturus batis*) which is a late-maturing species (Walker and Hislop 1998). However, because of fishing pressure, the skate assemblage is currently dominated by the early-maturing and smaller starry skate (*Amblyraja radiata*) (Walker and Hislop 1998). Fishing mortality also has contributed to the population declines of the winter skate (*Leucoraja ocellata*), barndoor skate (*D. laevis),* and little skate (*L. erinacea*), further supporting the theory that late maturing species are increasingly susceptible to exploitation (Johnson 1979, Brander 1981, Casey and Myers 1998, Frisk et al. 2002).

Historically skates and rays have not had a directed fishery in California. Their primary catch has resulted from incidental catch by nearshore trawl fisheries. Skates comprise over 90 % of the total elasmobranch catch in recent years. The total skate catch from 1948-1989 was distributed between central and northern California with Monterey and San Francisco comprising the majority of the catch (> 70%). However, northern California (Eureka, Crescent City and Fort Bragg) has increased their contribution to over 75% of the total skate catch over the last several years (Zorzi et al. 2001).

Fisheries in the eastern north Pacific (ENP) are in their infancy but are gaining momentum; further emphasizing the need for improved life history data for these species. Of the nine species of skates occurring in the ENP life history information is available for less than half, focusing on nearshore skate species including the big (*Raja binoculata*), and sandpaper (*Bathyraja kincaidii*) skates (Perez 2005, Matta 2005). Information on the remaining species is limited to taxonomic information and decryptions of egg cases (Cox 1963, Ebert and Davis *in press*). This lack of basic life history information is of concern because the recent closures of nearshore trawling forced fishing effort further offshore exposing deepwater skates like *B. trachura* to increased fishing pressure than in previous decades.

Additionally, significant relationships link body size and age at maturity suggesting that body size is a trait that can identify species potentially susceptible to exploitation (Frisk et al. 2001, Dulvy and Reynolds 2002). Walker and Hislop (1998) investigated spatial and temporal shifts in skate assemblage of the North Sea over time, concluding that there was a noticeable change in species composition favoring smaller species with low age at maturity. *Bathyraja trachura* was found to be a slow growing, moderately long lived species, attaining maturity at 77-86% of asymptotic length and therefore potentially susceptible to exploitation.

Although no directed fishery is targeting *B. trachura*, their presence as bycatch in other target fisheries and the presence of increased fishing pressure due to nearshore fishery closures indicate the need for management. The results I have provided can be used to establish minimum management protocols for *B. trachura*. However, caution is necessary when using these unvalidated age estimates for management purposes because of the inherent possibility for over or underestimation of age (Campana 2001, Cailliet & Goldman 2004).

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