AGE, GROWTH AND MORTALITY OF PATAGONIAN TOOTHFISH (*DISSOSTICHUS ELEGINOIDES*) CAUGHT OFF KERGUELEN

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Abstract

Ages of Patagonian toothfish (*Dissostichus eleginoides*) caught off Kerguelen in 1999 were estimated by reading transverse-sectioned otoliths. Randomly interspersed otoliths from reference collections were used to measure precision; relative bias for the age data was estimated to be –0.6 years and residual variance 2.9. Age distributions of toothfish caught by two vessels showed discrepancies due to gear-specific catchability, or differences in the available population with depth or season. Age–length keys were constructed for use in assessing toothfish catches made by trawlers and longliners at Kerguelen, and longevity was estimated to be 36 years. Total instantaneous mortality *Z* was estimated to be between 0.09 and 0.12. Significant differences in age-at-length data between sexes were found, estimating von Bertalanffy parameters for males to be L_∞ = 95.9, *K* = 0.12, t_0 = –4.6 and for females L_∞ = 103.5, *K* = 0.11, t_0 = –4.7.

Résumé

Estimation de l'âge des légines australes (*Dissostichus eleginoides*) capturées au large de Kerguelen en 1999 par lecture de coupes transversales d'otolithes. La précision est mesurée sur les otolithes choisis au hasard dans des collections de référence; le biais relatif affiché dans les données d'âge est estimé à –0.6 ans et la variance résiduelle à 2,9. Les distributions d'âge des légines capturées par deux navires affichent des divergences dues à la capturabilité selon l'engin ou à des différences entre la population disponible et la profondeur ou la saison. Des clés âge–longueur ont été construites pour l'évaluation des captures de légine effectuées par les chalutiers et les palangriers à Kerguelen. La longévité est ainsi estimée à 36 ans. La mortalité instantanée totale *Z* est estimée entre 0,09 et 0,12. D'importantes différences ont émergé dans les données de longueurs selon l'âge entre les sexes, portant l'estimation des paramètres de von Bertalanffy pour les mâles à L_∞ = 95,9, *K* = 0,12, t_0 = –4,6 et pour les femelles L_∞ = 103,5, *K* = 0,11, t_0 = –4.7.

Резюме

Возраст патагонского клыкача (*Dissostichus eleginoides*), пойманного у о-вов Кергелен в 1999 г., оценивался путем считки поперечных срезов отолитов. Включенные случайным образом отолиты из справочных коллекций использовались для измерения точности; оценка относительной систематической ошибки в данных по возрасту составила –0.6 лет, а остаточная дисперсия – 2.9. В распределении возраста особей клыкача, пойманных двумя разными судами, имеются расхождения, вызванные разной уловистостью снастей или различной доступной популяцией в зависимости от глубины или сезона. Были составлены размерно-возрастные ключи для использования при оценке уловов клыкача, полученных траулерами и ярусоловами у Кергелена; расчетная продолжительность жизни составила 36 лет. Общий мгновенный коэффициент смертности *Z* по оценке лежит в диапазоне

0.09–0.12. Были выявлены значительные различия между полами в данных о возрасте по длине, параметры Берталанфи для самцов составили $L_\infty = 95.9$, $K = 0.12$, $t_0 = -4.6$, а для самок – $L_\infty = 103.5$, $K = 0.11$, $t_0 = -4.7$.

Resumen

Se estimó la edad de la austromerluza negra (*Dissostichus eleginoides*) extraída en los alrededores de Kerguelén en 1999 mediante la lectura de secciones transversales de otolitos. A fin de asegurar la precisión, durante el proceso de la lectura se introdujeron al azar otolitos provenientes de colecciones de referencia; el error sistemático relativo de los datos de edad se estimó en –0.6 años y la varianza residual en 2.9. Se observaron discrepancias en la distribución de la edad de los peces capturados por dos barcos debido a la capturabilidad por arte de pesca, o las diferencias en las poblaciones disponibles según la profundidad o estación. Se construyeron claves edad-talla, a ser utilizadas en la evaluación de la captura de austromerluza de barcos arrastreros y palangreros en Kerguelén, y se estimó que la longevidad era de 36 años. Se estimó la mortalidad instantánea total Z entre 0.09 y 0.12. Se encontró que habían diferencias significativas entre los datos de edad por talla para machos y hembras, y los parámetros de von Bertalanffy estimados para machos fueron: $L_\infty = 95.9$, $K = 0.12$, $t_0 = -4.6$; y para hembras $L_\infty = 103.5$, $K = 0.11$, $t_0 = -4.7$.

Keywords: Patagonian toothfish, age–length key, ALK, Southern Ocean, notothenid, age determination, CCAMLR

Introduction

In contrast to early sealing and whaling activity, current large-scale exploitation in the Antarctic targets on krill and finfish populations. Extensive illegal fishing of Patagonian toothfish (*Dissostichus eleginoides*) has led to considerable concern that stocks are being over-harvested (SC-CAMLR, 1996). Toothfish is a valuable resource and is likely to continue to command a high price in world markets. The Convention on the Conservation of Antarctic Marine Living Resources is concerned with conserving the Antarctic ecosystem while allowing harvesting. In other parts of the world, however, over-harvesting of larger, commercially valuable species has led to the fishing down of marine food webs, leaving impoverished, less valuable ecosystems (Pauly et al., 1998).

To avoid this, the sustainable management of fisheries uses age data for modelling population age structure and estimating rates of population growth, mortality and recruitment (Jones, 1992). By monitoring these through time, fishery managers can detect trends indicating population juvenescence or risk of over-harvesting. They can also follow individual cohorts through time. By doing so, they can calculate rates of age-specific survival and mortality, and estimate age-specific fecundity by incorporating data on egg production within each age class. These age-specific vital rates can be used to elucidate life-history strategies. Moreover, by taking advantage of data on catch rates from fisheries and linking these to data on age composition, age-structured models can reconstruct the dynamics of exploited populations, to provide estimates of age-specific vital rates and predictions of absolute abundance of individual cohorts (Megrey, 1989).

These analyses depend on reliable age data, yet over-estimation of the age of younger fish and under-estimation of the age of older fish, documented particularly among inexperienced readers (Kimura and Lyons, 1991), can lead to biases in estimates of age structure and population vital rates. Moreover, variability in ageing precision can mask year-class strength (Fournier and Archibald, 1982), undermining cohort analyses. To guard against these, the methodology for age determination should be applied consistently across the sampled population and over a sequence of years while minimising sources of error (Morison et al., 1998). However quantitative estimates of bias and precision are also needed for data users to enable them to assess the error in the age data when deciding which analyses are appropriate (Kimura and Lyons, 1991).

This project presents the results of a collaboration between the Center for Quantitative Fisheries Ecology (CQFE) of Old Dominion University (ODU) and the Laboratoire d'Ichthyologie Générale et Appliquée of the Museum National d'Histoire Naturelle, in which the age of *D. eleginoides* caught around Kerguelen was estimated. Ageing error was estimated using collections of reference otoliths held at CQFE, age–length keys were produced for use in assessing the toothfish population at Kerguelen, and rates of population mortality and growth were estimated.

Methods

Observers sampled otoliths of 826 fish from the catch taken in March 1999 off Kerguelen between depths of 500 and 1 500 m by the longliner FV *Northern Pride*, and in August/September 1999 by the trawler FV *Kerguelen de Trémarec,* fishing in depths between 300 and 800 m. One otolith was randomly selected from each fish and prepared using a technique developed at CQFE specifically for toothfish otoliths. The otolith was baked in a Barnstead Thermolyne 1400 Furnace at 375°C for approximately 3–4 minutes until brown. Using the grinding wheel of a HillQuist Thin Section machine, each otolith was ground from the anterior end to give a transverse plane anterior of the nucleus. The plane provided a surface for mounting the otolith on a slide using Loctite© 349 adhesive, cured under UV light. The mounted otoliths were then ground from the posterior side to give a thick section, revealing a transverse plane through the otolith nucleus. The transverse plane was positioned between crenellations because otolith microstructure is frequently obscured within crenellations (Everson, 1980; Ashford, 2001). The revealed section was fine-ground and polished using a Crystalmaster 8 Machine with 30M and 3M Mark V Laboratory lapping film. Finally, polished sections were clarified and sealed using Flo-Texx© resin. Mounted sections were stored in slide boxes.

Sections were viewed by reflected light using a Leica MX8 microscope. To test for consistency with previous studies undertaken at CQFE, 52 slides from a South Georgia reference collection held at CQFE were added to the newly prepared sample slides. The reference set consisted of sections that had been repeatedly read: the mean age of the readings for each section was used as its reference age (Ashford, 2001). Reference and sample sections were pooled, randomly sorted, and allocated a random number. Ageing criteria used were those agreed at the CCAMLR Workshop on Estimating Age in Patagonian Toothfish (SC-CAMLR, 2001), tested in validation studies using strontium chloride marking of otoliths (Krusic-Golub and Green, 2001), marginal increment analysis (Horn, 2002) and modal length analysis (Ashford et al., 2002). The otoliths were read consecutively in order of random number by reader R_1. However, subsequent analysis revealed a trend towards younger ages in the order in which otoliths were read, indicating that R_1 changed criteria during the course of the study. In consequence, the sample sections were again pooled with sections from the reference set, sorted randomly, and re-read by another experienced reader (R_2) and a reader in training (R_t). Data generated by R_1 were not used in any further analysis.

Precision and accuracy relative to the CQFE reference otolith set were estimated by comparing reference ages and ages read by R_2 and R_t for all reference otoliths. To do this, an ANOVA randomised complete blocks design was used (Ashford, 2001):

$$y_{ij} = \mu + \tau_i + b_j + e_{ij} \qquad i = 1,2 \ldots t;\ j = 1,2 \ldots r \tag{1}$$

where μ = the general mean, τ_i = the effect of the *i*th level of the factor reading (three levels: reference age and ages read in this study), b_j = the effect of the *j*th level of the blocking factor fish, e_{ij} = the experimental error. The bias was estimated using the difference between the estimated general mean and estimated treatment mean $(y_{..} - y_{i.})$, and tested to see whether it was significant using a Tukey HSD test (α = 0.05). Precision was measured by estimating the variance of the residuals.

Age–length keys were constructed by building an age-at-length matrix using the length data taken by fishery observers. Using all the age data, the proportions of the population at each age were calculated (Fridriksson, 1934; Kimura, 1977):

$$\hat{p}_i = \sum_{j=1} \hat{l}_j \hat{q}_{ij'} \tag{2}$$

where p_i is the proportion of a population of age i = 1,2,3,...,n; l_j is the proportion of total length j measured in intervals of 10 cm; and q_{ij} is the proportion of fish of age i within an age subsample for a total length j.

To estimate the rate of instantaneous total mortality (Z), two methods were used: that of Royce (1972), in which the estimate of the number of cohorts in the population was taken as the age of the 99 percentile fish, to avoid the effect of outliers. In addition, a catch curve based on a negative exponential model was used:

$$N_t = N_0 e^{-Zt} \tag{3}$$

where N_t is the number of fish at age t, and N_0 is the number of fish in the first year class. Data were $\log_e$-transformed and fitted by the linearised model, allowing the slope to be used as an estimate of Z. As cohorts not fully recruited to the gear can bias mortality estimates, only those cohorts older than the mode were used, for which there was a clearly decreasing trend in abundance (Chapman and Robson, 1960; Barbieri et al., 1994).

To estimate growth, data from both vessels were used, fitting the von Bertalanffy model separately by least squares for each sex, and to the data pooled for both sexes. The model H_Ω (equation 4) was generated, in which parameters were fitted by sex, and the model H_w (equation 5), in which parameters were fitted using the pooled data:

$$H_\Omega : l_{ij} = L_{\infty i}\left(1 - e^{-K_i\left(t_{ij} - t_{0i}\right)}\right) \quad (4)$$

$$H_w : l_{ij} = L_\infty\left(1 - e^{-K\left(t_{ij} - t_0\right)}\right) \quad (5)$$

where l_{ij} is the total length of the *j*th fish from the *i*th area, L_∞ is the mean maximum length, t_0 is the theoretical age at which length = 0, and K is the Brody growth coefficient, governing the rate at which L_∞ is approached. Residuals were examined visually for error trends, and for normality using the Shapiro–Wilks test ($\alpha = 0.05$). The data departed significantly from normality, but this was mostly due to kurtosis. Since the data remained reasonably symmetric, and $n_i \geq 10$ for ages $i = 2 \ldots 17$, parameter estimates should be robust to violations of the normality assumption (Kimura, 1980). To test for differences between sexes, likelihood ratio (*LR*) tests were undertaken to select the model which best represented the data. Being more complex, H_Ω could be expected to describe the data best: some criterion was needed to test whether this was sufficient to justify selection over the simpler model H_w. *LR* (Λ) can be used to generate the test statistic:

$$-2\log(\Lambda) = -N\log\left(\frac{\sigma_0^2}{\sigma_{ai}^2}\right) \quad (6)$$

which has a chi-squared distribution, and can be used to test for significant differences between models (Kimura, 1980).

Results

Readers R_2 and R_t estimated the ages of 825 of the 826 fish sampled. Data for total length were missing for one fish, and the otoliths were missing for another. The ages of eight fish were re-read as potential outliers to the von Bertalanffy model; second readings differed little and the original ages were kept. For the reference otoliths, the bias of R_2 was estimated to be –0.60 years relative to reference ages, and R_t to be 0.17 years (Figure 1); neither bias was significant (Table 1). R_t was less consistent (residual variance = 6.8) than R_2 (residual variance = 2.9), and showed evidence of a small trend in the order of reading. To avoid consequent biases in estimates of von Bertalanffy parameters and Z, only age readings from R_2 were used in the further analysis.

Of the catches made by the longliner *Northern Pride*, 38% were younger than 9 years compared to nearly 80% of the fish caught by the trawler *Kerguelen de Trémarec* (Figure 2). Fish appeared to have recruited fully to the catch by age 5–6 for the *Northern Pride*, and by age 4 for the *Kerguelen de Trémarec*. Since the ages of fish sampled were distributed differently between vessels, and no estimates of gear-specific catchability-at-age (q_g) were available to correct for the vessel effect, age–length keys were constructed separately for each vessel (Table 2). Longevity was found, as measured by the 99 percentile, to be 36 years for fish collected from the *Northern Pride* and 27 years for those collected from the *Kerguelen de Trémarec*.

Using the data from the *Northern Pride*, total mortality was estimated as $Z = 0.12$ (Royce, 1972), and $Z = 0.09$ (SE = 0.01; $R^2 = 0.88$) by fitting the negative exponential model to age cohorts 5 years and older. For the *Kerguelen de Trémarec*, the respective estimates were $Z = 0.16$ and $Z = 0.14$ (SE = 0.02; $R^2 = 0.77$). Fitting the von Bertalanffy model to the age-at-length data, small differences were found in parameter estimates between sexes (Figure 3, Table 3), which were significant on testing (Table 4).

Discussion

The method of age estimation developed at CQFE was applied to process large numbers of specimens and provide quantitative estimates of variability in age data. The processed otoliths constitute a reference set for *D. eleginoides* caught off Kerguelen, that can be used to underpin a quality assurance protocol for future age studies, to detect biases and monitor precision. Residual variance gives a measure of proficiency, by which a reader can measure personal performance. Storage of sectioned reference otoliths on slides is convenient and the large number in the reference collection will reduce wear and recognition effects.

The trainee reader R_t showed a higher residual variance than R_2, reflecting the importance of experience in achieving consistency. Data from R_2 showed little expansion in residual variance with age, indicating that error was principally due to interpretation of annuli laid down before maturity. Changes in criteria, as found over the course of this study for R_1 and to a lesser extent R_t, led to both bias and increased precision error. Changing criteria by R_1 were not originally detected using reference otoliths, despite $n_{ref} = 52$ used, but plots showing the order of reading of samples clearly showed the trend and have been incorporated in the quality control procedure. A pre-requisite was that otoliths were randomly sorted before reading: without this, trends over the course of a study would have been difficult to detect.

The age distribution of fish caught by the *Northern Pride* showed strong discrepancies from those caught by the *Kerguelen de Trémarec*. Sampling effects are potentially important in generating biases in estimates of age structure (Morison et al., 1998), and the differences may have reflected the gear used as well as depth and season fished. The central assumption of an age–length key is that samples are representative of the original population. If they are not, the age–length key will give biased results (Ricker, 1975), and estimates of growth and mortality parameters will be similarly biased. Where samples are taken randomly from the catch, they will represent the removals from the original population by each gear, rather than the original population itself. However, the catch C_{gij} taken in each age(i)-length(j) cell using gear g can be viewed as related to the available fished population (N_{ij}) by gear-specific catchability (q_{gij}) and effort (f) in the relationship $C_{gij} = q_{gij} f N_{ij}$. Estimates of q_{gij} may therefore correct for biases in the catch when effort is known. The two age–length keys presented in this study reflect the removals taken under $q_{trawler}$ and $q_{longliner}$, as well as differences in the available population (N_{ij}) with depth and season. Estimates of $q_{trawler}$ and $q_{longliner}$ would allow N_{ij} to be estimated. Moreover, if the effects due to depth and season account for enough overall variance in N_{ij}, their estimation may allow age–length keys to be applied reliably over the fishing area and between years.

Differences in q between the two vessels, as well as availability with depth, most likely explain the discrepancies in estimates of Z between gears. Because more older fish appear to be available and vulnerable to longlining, the estimates based on the catch by the *Northern Pride* are probably less biased. However, they may still overestimate mortality if q decreases with age once fish are older than 4–6 years, and are best considered as upper bounds of the true mortality rate. Moreover, the estimates depend on the assumption of discrete populations: an influx of older fish through migration may result in an increase in apparent survival, whereas their departure would result in an overestimate of mortality similar to the effect of decreasing q with age.

Catchability may also change over time, driven by evolving technology, fishing strategies, or market demand for specific size classes, for instance to improve the quality of fillets. Demand for certain smaller size classes, rather than changes in growth rate, could help explain the decline in values of L_∞, especially for females, when compared to a pooled sample of toothfish taken by longliner and trawler (Ashford, 2001) off Kerguelen in 1997 (L_∞ for males = 105.9 cm and for females = 162.9 cm), and another sample taken mostly in 1996/97 (Horn, 2002) in the western Pacific sector of the Southern Ocean (L_∞ for males = 134.3 cm and for females = 158.7 cm). However, there is little evidence to support this explanation. Instead, it is more likely longliners in particular would continue to take large fish where available, and the decline in L_∞ therefore reflects a trend in the age-at-length distribution of toothfish at Kerguelen as a result of fishing.

Conclusions

1. Longevity measured by the 99 percentile was 36 years.

2. Total mortality (Z) was estimated to be between 0.09 and 0.12.

3. Age-at-length was significantly different between sexes.

4. Von Bertalanffy parameter estimates for males were $L_\infty = 95.9$, $K = 0.12$, $t_0 = -4.6$; for females $L_\infty = 103.5$, $K = 0.11$, $t_0 = -4.7$.

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Table 1: Results from analysis of variance using randomised complete block design to measure precision bias and variability of age data from n = 52 reference otoliths. Levels of treatment factor were reader 2, reader in training, reference age (α = 0.05).

Source	df	MS	*F*	*Pr* > F
Reading	2	8.5	1.3	0.280
Block (fish)	51	262.8	40.0	<0.0001
Error	102	6.6		

Table 2: Age–length keys for *Dissostichus eleginoides* using (a) age data sampled from the *Northern Pride* in March 1999, and (b) age data sampled from the *Kerguelen de Trémarec* in August/September 1999. TL = maximum total length in each 10 cm grouping (i.e. TL = 40 is for grouping 31–40 cm). Prop. = proportion.

(a) *Northern Pride*

	Age																			
TL	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
40																				
50			1	1																
60				2	4	2	4			1										
70				3	9	16	7	4	6	1	1	1								
80				2	6	15	20	10	13	6	10	3	4	1	1		3	1		3
90				2		6	8	5	9	16	7	9	10	7	10	7	9	7	3	10
100					1			2	2	2	4	4	9	3	6	8	7	8		2
110										1	1	2		1	5	6	1	3	2	1
120														1			1	1	1	
130														1						
Total			1	10	20	39	39	21	30	27	23	19	23	14	22	21	21	20	6	16
Prop.			0.00	0.02	0.04	0.08	0.08	0.04	0.06	0.06	0.05	0.04	0.05	0.03	0.04	0.04	0.04	0.04	0.01	0.03

TL	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36+	Total
40																		
50																		2
60																		13
70																		48
80		1																99
90	5	4	2	2	2	1	1	1	1	2	2	1						149
100	4	8	10	3	4	3	5	5	4	3	6	2	2	2	1		4	124
110		1	1	2		2			2	3	1	1	1			1	1	39
120			1	1			2		1	1						1	2	13
130			0	1											1			3
Total	9	14	14	9	6	6	8	6	8	9	9	4	3	2	2	2	7	490
Prop.	0.02	0.03	0.03	0.02	0.01	0.01	0.02	0.01	0.02	0.02	0.02	0.01	0.01	0.00	0.00	0.00	0.01	

(continued)

Table 2 (continued)

(b) *Kerguelen de Trémarec*

	Age																			
TL	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
40																				
50				3																
60			19	19	24	5	1		1											
70			6	9	27	21	11	8	3	2	1						1			
80				3	7	15	22	16	12	7	3	2	1	1		1			1	
90					2	5	3	6	6	6	4	5	2		3	1	6	2	5	1
100								2						1	1	2	1	1	1	1
110																				
120																				
130																				
Total			25	34	60	46	37	32	22	15	8	7	3	2	4	4	8	3	7	2
Prop.			0.07	0.10	0.18	0.14	0.11	0.10	0.07	0.04	0.02	0.02	0.01	0.01	0.01	0.01	0.02	0.01	0.02	0.01

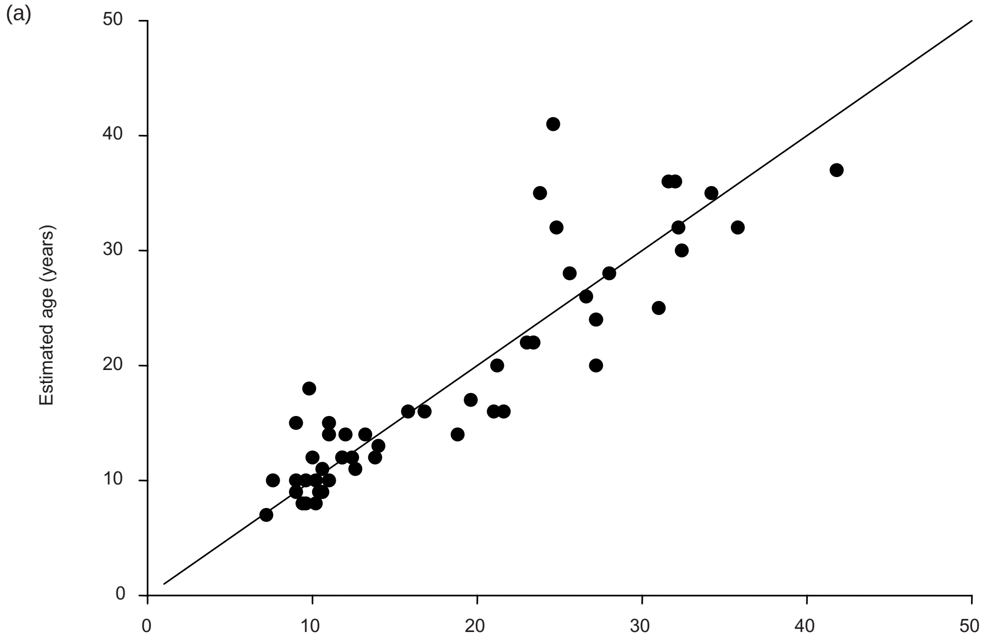
TL	20	21	22	23	24	25	26	27	28	29	30	31	Total
40													
50													3
60		1											70
70													89
80				1				1					93
90		1			1	1		1			1	1	63
100	1		1		1				1	1			15
110						1							1
120													
130													
Total	1	2	1	1	2	2		2	1	1	1	1	334
Prop.	0.00	0.01	0.00	0.00	0.01	0.01		0.01	0.00	0.00	0.00	0.00	

Table 3: Estimates of von Bertalanffy growth parameters for male and female *Dissostichus eleginoides* caught off Kerguelen. Standard errors in brackets (n_m = 388 males, n_f = 436 females).

	L_∞		K		t_0	
Pooled	98.2	(1.0)	0.13	(0.01)	–4.1	(0.6)
Male	95.9	(1.3)	0.12	(0.01)	–4.6	(0.7)
Female	103.5	(1.9)	0.11	(0.01)	–4.7	(0.9)

Table 4: Likelihood ratio tests comparing von Bertalanffy parameter estimates for male and female *Dissostichus eleginoides* from Kerguelen (n = 824, α = 0.05).

Hypothesis	Constraints	Sum of squares	$-N \log\left(\frac{\sigma_\Omega^2}{\sigma_\omega^2}\right)$	df	$<p$
$H\Omega$	none	53590.6			
$H\Omega 4$	all	60427.6	98.9	3	0.001



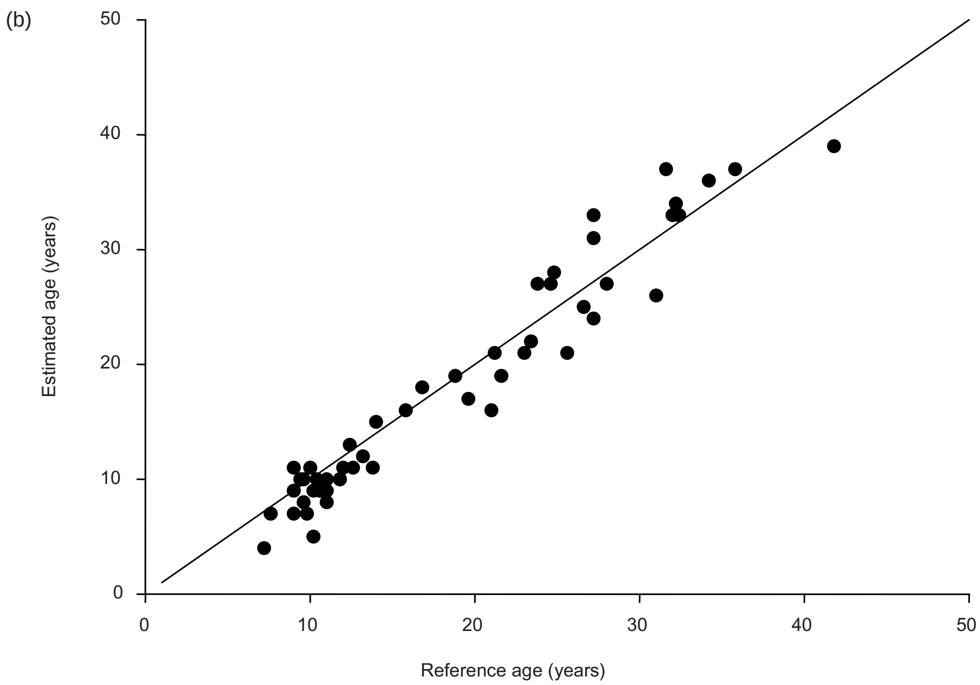


Figure 1: Ages of *Dissostichus eleginoides* estimated by (a) a reader in training (R_t) and (b) an experienced reader (R_2) from otolith sections from a South Georgia reference collection, compared to reference ages.

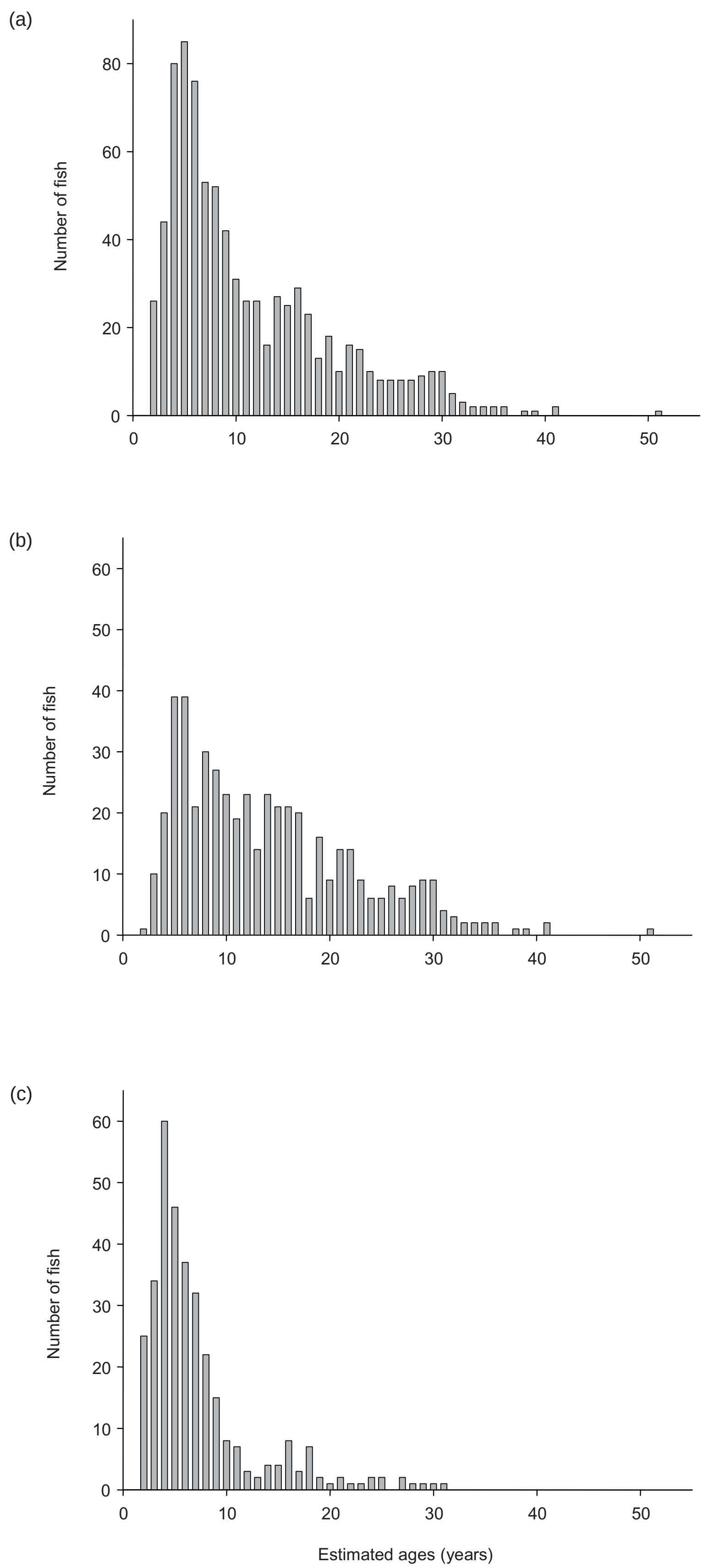


Figure 2: Age structure of *Dissostichus eleginoides* caught off Kerguelen by the longliner *Northern Pride* and trawler *Kerguelen de Trémarec*, showing (a) all data pooled; (b) *Northern Pride* data; and (c) *Kerguelen de Trémarec* data.

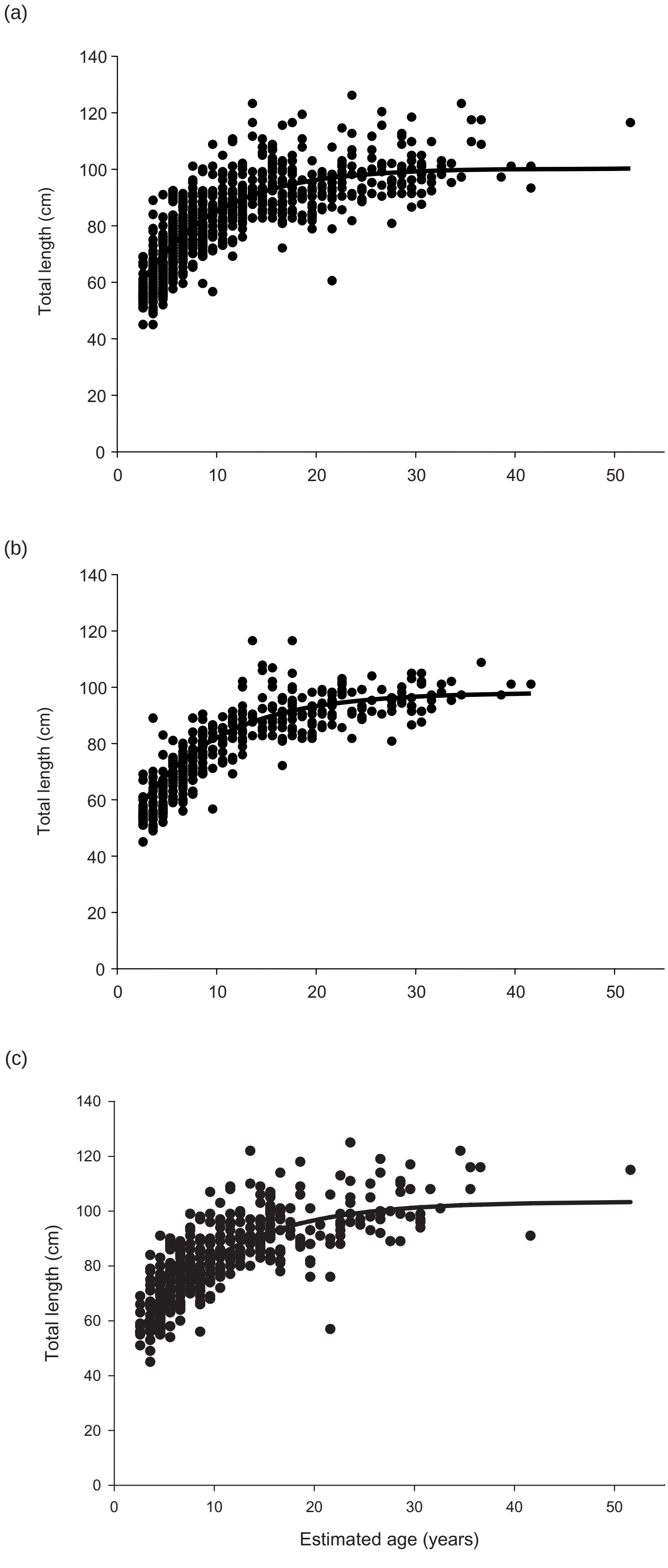


Figure 3: Von Bertalanffy model fitted to age-at-length data for *Dissostichus eleginoides* caught off Kerguelen: (a) all data pooled; (b) males; (c) females. Ages are corrected for overall bias estimated for reader R_2.

Liste des tableaux

Liste des figures

Список таблиц

Список рисунков

Lista de las tablas

Lista de las figuras