SIZE AT SEXUAL MATURITY OF PATAGONIAN TOOTHFISH (*DISSOSTICHUS ELEGINOIDES*)

I. Everson and A. Murray
British Antarctic Survey
High Cross, Madingley Road
Cambridge CB3 0ET, United Kingdom

Abstract

Analyses of size at sexual maturity were undertaken on samples of Patagonian toothfish (*Dissostichus eleginoides*) caught in the commercial fishery within Subarea 48.3. The results for 1996 indicate that L_{m50} occurs at 78.5 cm total length for male and 98.2 cm for female fish. In 1997 the results for male fish were essentially the same. For female fish there is evidence that in 1997 a significant proportion, 25 to 43%, of sexually mature fish were not coming into spawning condition. This introduces a bias leading to the overestimation of L_{m50} calculated by conventional methods. Further analysis allowing for this bias indicates that L_{m50} for female fish in 1997 was no different to that for 1996. The implications of this phenomenon are discussed.

Résumé

Analyses de la taille à la maturité sexuelle d'échantillons de légine australe (*Dissostichus eleginoides*) capturés par la pêche commerciale de la sous-zone 48.3. Pour 1996, les résultats indiquent que L_{m50} correspond à 78,5 cm de longueur totale chez les mâles et 98,2 cm chez les femelles. Pour 1997, les résultats sont pratiquement identiques pour les mâles alors que pour les femelles, il semble qu'une proportion importante (de 25 à 43%) de poissons ayant atteint la maturité sexuelle n'étaient pas en condition de reproduction. Ceci introduit un biais tendant à surestimer L_{m50} calculé par les méthodes conventionnelles. Une nouvelle analyse tenant compte de ce biais indique que pour les femelles, la valeur de L_{m50} en 1997 ne diffère pas de celle de 1996. Les conséquences de ce phénomène sont examinées.

Резюме

Был проведен анализ размера при достижении половозрелости по экземплярам патагонского клыкача (*Dissostichus eleginoides*), выловленным в ходе коммерческого промысла в Подрайоне 48.3. Результаты за 1996 г. указывают на то, что L_{m50} достигается при общей длине 78,5 см для самцов и 98,2 см для самок. В 1997 г. результаты для самцов были в основном такими же. Для самок есть свидетельства того, что в 1997 г. значительная пропорция (25–43%) половозрелых особей не была готова к нересту. Это приводит к смещению, вызывающему завышенную оценку L_{m50} при вычислении обычными методами. Дальнейший анализ с учетом этого смещения показывает, что в 1997 г. L_{m50} для самок идентичен показателю за 1996 г. Обсуждаются возможные последствия этого явления.

Resumen

Se analizaron muestras del bacalao de profundidad (*Dissostichus eleginoides*) capturado en la pesquería comercial que operó en la Subárea 48.3 para determinar la talla de madurez sexual. Los resultados de 1996 indican que L_{m50} se alcanza cuando la longitud total de los peces machos es de 78,5 cm y la de las hembras, 98,2 cm. En 1997 se obtuvieron resultados básicamente similares para los machos. En lo que respecta a los peces hembra, existen pruebas de que en 1997 una proporción significativa (25 a 43%) de peces que habían alcanzado la madurez sexual no habían ovulado. Esto introdujo un sesgo en los resultados y causó una sobrestimación del valor L_{m50} calculado según los métodos convencionales. Otros análisis que han tomado en cuenta este sesgo indican que en 1997 L_{m50} para los peces hembra fue igual al valor de 1996. En este trabajo se consideran las consecuencias de este fenómeno.

Keywords: Patagonian toothfish, *Dissostichus eleginoides*, size, males, females, sexual maturity, bias, overestimation, Subarea 48.3, CCAMLR

INTRODUCTION

Antarctic nototheniid fish typically produce large yolky eggs and mature at about half their maximum length (Kock and Everson, 1998). The process of yolk deposition typically takes more than a year (Everson et al., 1996), with the final maturation process leading to an enlarged ovary of about 20% of the fish total mass. Spawning occurs in the period July to September (Kock and Kellermann, 1991) although the precise location of spawning grounds is unknown. Knowledge of the rate of gonad maturation and the size of the fish when first maturation occurs is important information in stock assessment.

The Patagonian toothfish (*Dissostichus eleginoides*) has been harvested commercially around South Georgia over the past decade, but since it occurs in deep water there is still a dearth of basic information on its ecology. There is still no precise information on the reproductive cycle. This was highlighted at the 1997 meeting of the CCAMLR Working Group on Fish Stock Assessment (WG-FSA), where there was considerable uncertainty over the size at sexual maturity.

The CCAMLR Scheme of International Scientific Observation, by providing for coverage of the whole fishing fleet operating in Subarea 48.3, has been an extremely important source of data and information. In this paper, data from the observer program have been analysed to provide a clearer indication of the size at which the fish become sexually mature in the South Georgia region.

METHODS

The data used for this study were collected as part of the CCAMLR Scheme of International Scientific Observation. All the data were collected on commercial longlining vessels operating within Subarea 48.3 (South Georgia). Data were submitted to, and stored in, the CCAMLR database. Files containing all data from the 1996 and 1997 calendar years were prepared by the CCAMLR Data Manager and provided for the purpose of this analysis.

The data used in this analysis were total length, sex and maturity stage. Maturity stage was determined according to the five-point scale of Kock and Kellermann (1991). Descriptions of the maturity stages are set out in Table 1. Fish were considered to be sexually mature if the gonad was in maturity stage 3 to 5 (Everson et al., 1996).

The data were grouped into periods of two months and into 2 cm length groups from <62 cm to 128–130 cm to allow reasonable numbers of fish within each group. The periods used were March/April, May/June and July/August. The only exception to this was that, due to the closure of the fishery, there were no data for August 1996; this category therefore only contains data from July 1996.

Models were fitted to data using the Generalised Linear Model (GLM) and non-linear modelling facilities in Genstat (Payne et al., 1997). The logistic equation

$$p = \left(\frac{1}{1 + e^{(-\alpha + \beta L)}} \right)$$

is described by Ni and Sandeman (1984), where p is the estimated proportion of fish in a category, L is the total length in centimetres (the average total length of fish in the groups described above was used in computations) and α and β are coefficients. The proportion of fish that were sexually mature was modelled using a GLM with logit link function (linear in length) and binomial error distribution for counts. The model form used by Genstat is given by

$$\ln\left(\frac{p}{1-p} \right) = \alpha + \beta L \, .$$

We refer to this as logistic curve (asymptote = 1). The length at which 50% of the population were mature (L_{m50}) was determined from the fitted curves. Genstat procedure 'FIELLER' (Lane, 1993) was used to estimate L_{m50} together with fiducial limits (≡ confidence limits) for standard logistic curves (see Finney, 1978, Chapter 4 for method) from the fitted logistic GLM.

Genstat procedure 'PROBITANALYSIS' (Payne, 1993) was used to fit logistic models with an additional parameter for non-response (usually called 'immunity' in the language of bioassay – see Finney, 1978, Chapter 20) to cater for the situation where a proportion (*propn*) of fish which were sexually mature were not coming into spawning condition. We refer to this as logistic curve (asymptote unconstrained). The procedure also provided estimates of L_{m50} (with standard errors) for 'spawners' based on an upper asymptote of *1-propn*. An estimate of population L_{m50} (with standard errors), that is the point on the curve where 50% of the total population should

Table 1: Macroscopic description of maturity stages (Kock and Kellermann, 1991).

Maturity Stage	Description
Female:	
1. Immature	Ovary small, firm, no eggs visible to the naked eye.
2. Maturing virgin or resting	Ovary more extended, firm, small oocytes visible, giving ovary a grainy appearance.
3. Developing	Ovary large, starting to swell the body cavity, colour varies according to species, contains oocytes of two sizes.
4. Gravid	Ovary large, filling or swelling the body cavity, when opened large ova spill out.
5. Spent	Ovary shrunk, flaccid, contains a few residual eggs and many small ova.
Male:	
1. Immature	Testis small translucent, whitish, long, thin strips lying close to the vertebral column.
2. Developing or resting	Testis white, flat, convoluted, easily visible to the naked eye, about ¼ length of the body cavity.
3. Developed	Testis large, white and convoluted, no milt produced when pressed.
4. Ripe	Testis large, opalescent white, drops of milt produced under pressure or when cut.
5. Spent	Testis shrunk, flabby, dirty white in colour.

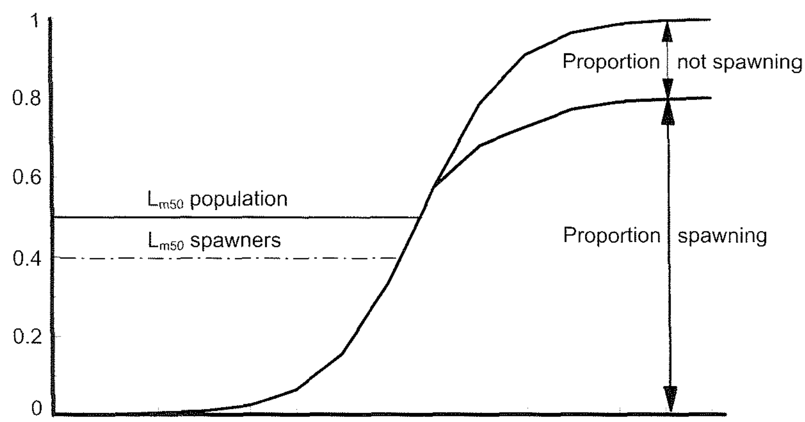

Figure 1: Diagrammatic representation of a situation whereby only 80% of all sexually mature fish come into spawning condition.

have developed at least to maturity stage 3, was interpolated using the fitted curve. The relationships of these parameters are indicated in Figure 1. Without the modification of the extra parameter, in the situation where a large proportion of sexually mature fish do not come into spawning condition, the logistic curve is pulled to the right and may fail to reach an asymptote within the range of the data. This can lead to a serious upwards bias in the estimated L_{m50}.

Both the FIELLER and PROBITANALYSIS Genstat procedures use logistic GLMs, the latter with additional ('immunity') parameter(s) to allow for an asymptote of less than 1.0. Models were fitted separately to each year per two-month dataset and to a combined dataset with terms to allow for separate values of L_{m50} and slopes for years (1996 versus 1997) and/or two-month periods, or separate year combined with two-month periods (six levels). Significance of model terms was assessed by deviance ratio tests (asymptotically equivalent to *F*-tests) using output from Genstat GLM fits.

RESULTS

Males

The results for male fish are plotted in Figure 2 along with the fitted curves. The values of L_{m50} and associated 95% confidence (fiducial) limits from analyses undertaken separately on each

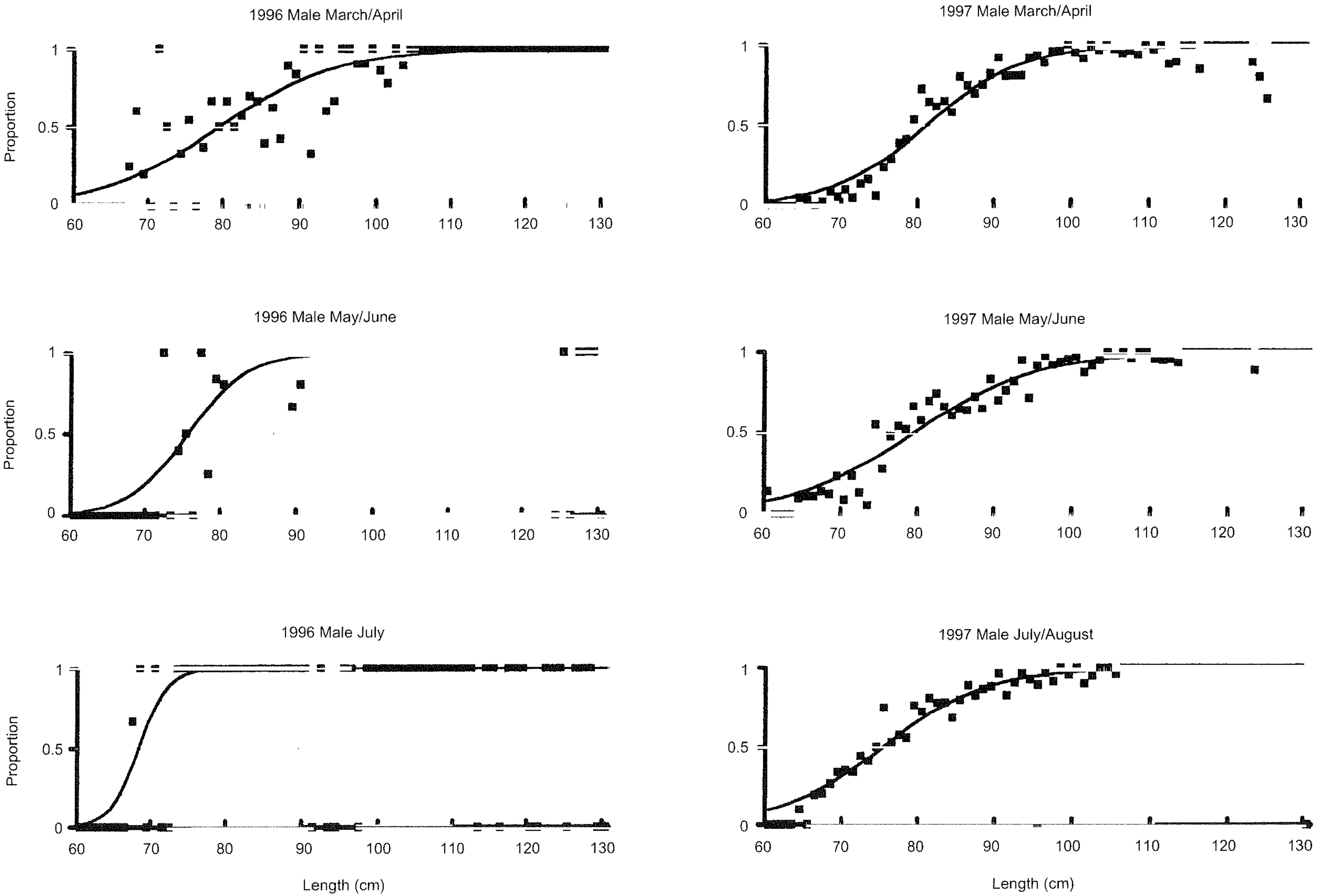

Figure 2: Proportion of male fish coming into spawning condition plotted against length. The fitted line is constrained to an asymptote of one.

Table 2: L_{m50} and 95% confidence (fiducial) intervals estimated from fitted logistic curves (asymptote = 1) using the FIELLER method for male fish over the two seasons.

Months	L_{m50}	Confidence Limit		n
		Lower	Upper	
March/April 1996	79.0	76.5	81.1	467
May/June 1996	75.2	72.1	77.6	275
July 1996	67.8	60.2	72.4	124
March/April 1997	80.6	79.8	81.4	2 220
May/June 1997	79.0	77.6	80.2	1 592
July/August 1997	74.9	73.7	76.0	1 523

two-month group are shown in Table 2. Most of the results are consistent with an L_{m50} value of between 75 and 80 cm. The only exception to this is from the July 1996 dataset, where the result appears unusually low; this is probably an artefact arising from the small number of data points which fall in the middle of the curve. (This point was highlighted as a warning indicator by the Genstat program during the analysis on the combined dataset.) The results from the PROBITANALYSIS procedure gave L_{m50} values very close to the FIELLER estimates, indicating that nearly all sexually mature fish were coming into spawning condition. This indicates that L_{m50} is correctly estimated by the FIELLER method. The only period when a significant proportion of fish appeared to be failing to come into spawning condition was during March and April 1997 ($p < 0.001$). However, since the proportion coming into spawning condition at that time was 96%, the effect would be negligible at the population level.

Analysis of the combined dataset for males, omitting the small, apparently unusual set of data from July 1996, gave no statistically significant difference ($p > 0.05$ from deviance ratio tests) in any parameter between years. Including the July 1996 data gave a statistically significant ($p < 0.002$ from deviance ratio test) intercept parameter for 1996 versus 1997 in the model – but the statistical significance is mainly due to the large total sample size as the effect was negligible from a biological point of view. A combined estimate for the dataset, excluding the small sample from July 1996, gives a best estimate of L_{m50} = 78.5 cm with 95% confidence (fiducial) limits of 77.9 and 79.0 cm.

Females

The results for female fish are plotted in Figure 3 along with the fitted curves. The results for 1996 are described well by the logistic curve (asymptote = 1), even though, as is the case for male fish, there are only sparse data in the middle of the curve for the July period. The results from the PROBITANALYSIS procedure (logistic curve, asymptote unconstrained) using the 1996 data gave estimates of zero for the extra parameter for non-response, indicating that most sexually mature fish were coming into spawning condition during that season. The estimated values of L_{m50} and associated 95% confidence (fiducial) limits are shown in Table 2.

The fitted logistic curves (asymptote = 1) for female fish for all pairs of months in 1997 do not accurately follow the trend in the distribution because they are constrained to reach an asymptote at 1.0. In all three cases, around the turning point where p = 0.5, the curve, indicated by the broken line in Figure 3, passes to the right of the distribution of data. This implies a higher L_{m50} than would be suggested by inspection. This pattern is consistent with there being a substantial proportion of sexually mature fish not coming into spawning condition. The fitted lines and L_{m50} values estimated for the 1997 data using the asymptote unconstrained PROBITANALYSIS method are clearly better than the fitted curves (asymptote = 1) for female fish. The differences are shown in Figure 3 and estimated L_{m50} values in Table 3. In every case for 1997 there was a highly statistically significant ($p < 0.001$) improvement to the model fit by including the extra parameter for non-response.

For the combined female dataset, a model with common slope, a single L_{m50} for 1996 with zero non-response, separate L_{m50} and non-response parameters for March/April, May/June and July/August 1997 fitted extremely well. There was no significant improvement to the model by allowing separate slope estimates for the different periods. The separate L_{m50} parameters are required to be fitted because of the parameterisation used internally in the Genstat PROBITANALYSIS procedure, but it can be seen from Table 3 that the confidence limits for the estimated values of

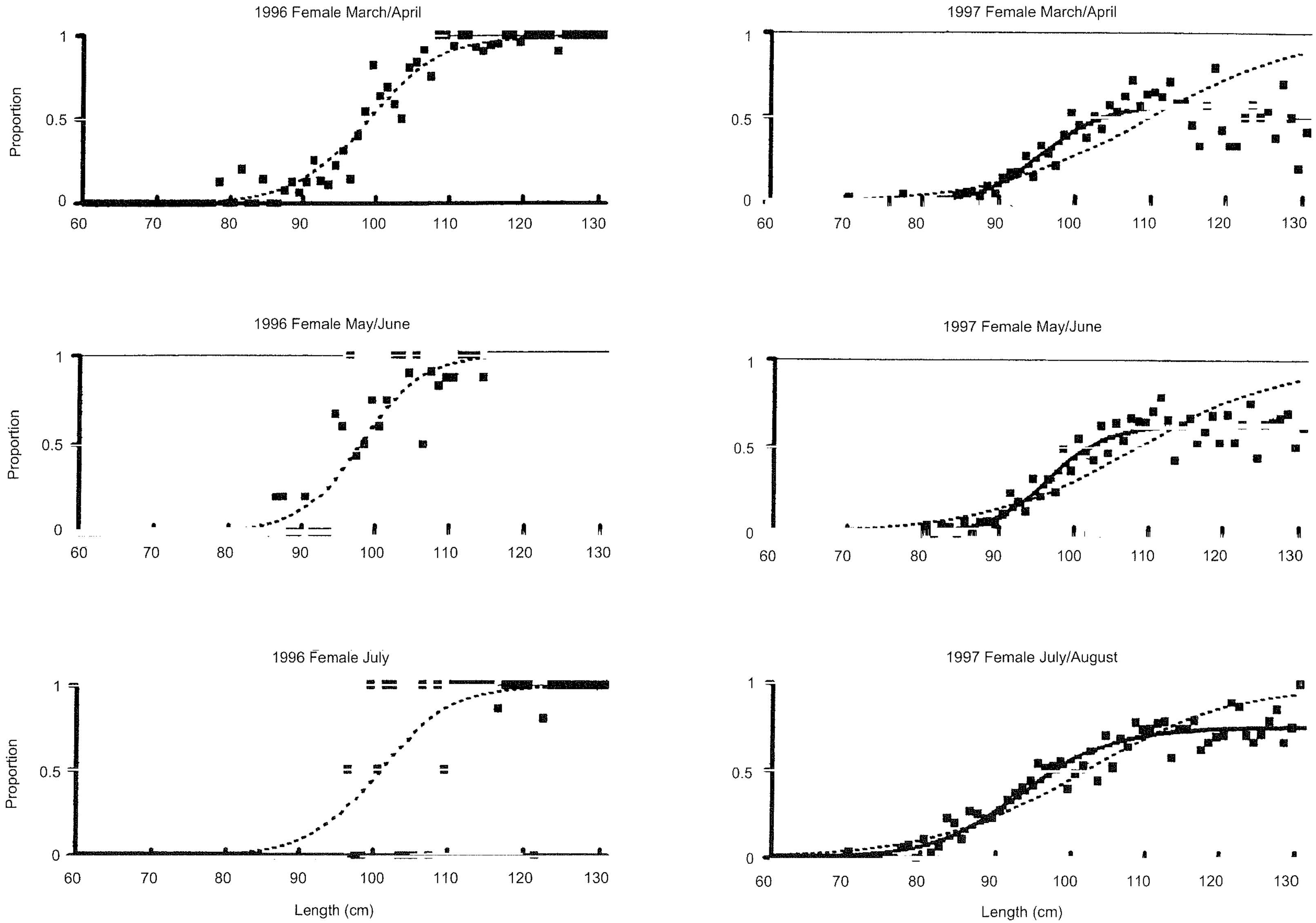

Figure 3: Proportion of female fish coming into spawning condition plotted against length. The broken line is for the fitted curve constrained by an asymptote of one. The solid line is for the fitted curve unconstrained by asymptote and fitted by the procedure PROBITANALYSIS.

Table 3: L_{m50} and 95% confidence (fiducial) intervals estimated from fitted logistic curves (asymptote = 1) using the FIELLER method for female fish and comparisons with the estimates adjusted for non-response using the logistic curves fitted by Genstat procedure PROBITANALYSIS (asymptote unconstrained) for 1997.

Months	L_{m50} FIELLER Limits	% Mature not in Spawning Condition	L_{m50} PROBIT-ANALYSIS	*n*
March/April 1996	98.5 (97.0–99.8)	0	no change	617
May/June 1996	97.5 (95.6–99.2)	0	no change	374
July 1996	100.4 (94.7–104.2)	0	no change	108
March/April 1997	110.6 (109.0–112.4)	43	98.8 (96.3–101.3)	2 089
May/June 1997	108.7 (107.3–110.2)	37	99.0 (98.1–99.9)	1 786
July/August 1997	101.7 (100.4–103.1)	25	95.9 (94.3–97.6)	1 721

population L_{m50} overlap with each other and with the estimates for 1996. This, together with the lack of evidence for any change in the slope of the response, suggests that there is very little evidence for any significant change in population L_{m50} over time in these data. Analysis of all data from 1996 gave an estimated L_{m50} = 98.2 cm with 95% confidence (fiducial) limits of 97.1 and 99.3 cm and this estimate is consistent with all the estimates in Table 3 (taking into account the confidence limits), suggesting a 'best' estimate of 98.2 cm for all females in both years.

DISCUSSION

The primary aim of the study was to determine L_{m50}, the size at which 50% of the fish become sexually mature. This is an important stock assessment parameter in determining the spawning stock biomass.

Results from the separate analyses of data from male fish within the two-month groups, but excluding the results for July 1996 for the reasons stated, fall within the range 74.9 to 80.6 cm. That range encompasses the value estimated by WG-FSA at its 1997 meeting (L_{m50} = 75.73) (SC-CAMLR, 1997), although it is outside that from the combined analysis reported here, which, for the same data, gave a mean of 78.5 and confidence limits of 77.9 and 79.0 cm. We consider this latter value to be a better estimator of the population L_{m50} than that given in SC-CAMLR (1997).

The results in Table 2 indicate that L_{m50} for male fish is declining in successive months. We offer no explanation for this but note that it may be a result of larger fish maturing earlier or an artefact of the sampling regime.

In the case of female fish the situation is more complicated. The 1996 data point to an L_{m50} of 98.2 cm with 95% confidence limits of 97.1 and 99.3 cm irrespective of whether the FIELLER or PROBITANALYSIS method is used. However, for 1997 the simple logistic (asymptote = 1) analyses do not provide a good fit to the data. A much better fit is afforded by the logistic curve (asymptote unconstrained) PROBITANALYSIS procedure which provides L_{m50} estimates indistinguishable from those for 1996. This analysis suggests that there is no evidence to support any change in the estimated L_{m50} between years.

The need to add a parameter to account for the proportion of sexually mature female fish that are not coming into spawning condition in 1997 indicates an ecological difference in the situation between the two years. We consider two possible interpretations. Either that a significant proportion of mature fish failed to spawn in 1997, or alternatively, there was a delay in the final maturation of female fish. In the terminology of Figure 1 the proportion not spawning declined progressively through each two-month period in 1997, which leads us to the tentative conclusion that the maturation process was probably delayed in that year. The July/August period falls well within the generally accepted spawning period for the species (Kock and Kellermann, 1991), which suggests that around 25% of female fish did not spawn in 1997.

Incomplete spawning is not an unusual phenomenon for fish. Everson et al. (1996), working on the channichthyid *Champsocephalus gunnari*, and Livingston et al. (1997), working on hoki (*Macruronus novaezelandiae*) found similar situations. None of these would qualify as partial or fractional spawners as defined by West (1990), because it appears that some individuals are not spawning at all during a season rather than producing limited numbers of oocytes for a series of separate spawning bouts. The nature of this process could be determined from a histological examination of the ovaries; unfortunately, this was not part of the sampling protocol but could be investigated in the future.

There is a further consequential effect arising from this phenomenon which may affect stock assessments. In seasons when all fish do not come into spawning condition the true spawning stock biomass will be less than the biomass of sexually mature fish. Antarctic fish typically produce relatively small numbers of large yolky oocytes, and if this output is reduced, because not all fish are spawning, this could affect larval production. Arising from this there may be an effect on recruitment. In answering one question, that related to L_{m50}, we have thus brought to light a further potential difficulty.

ACKNOWLEDGEMENTS

The data used for this analysis were obtained from the CCAMLR Scheme of International Scientific Observation. We would like to acknowledge the dedication of all observers in providing a valuable dataset for these analyses. We also thank Eric Appleyard of the CCAMLR Secretariat for providing us with the data and responding quickly to queries. Stuart Hanchet and an anonymous referee provided useful improvements on an earlier draft of the manuscript and this is gratefully acknowledged.

REFERENCES

Everson, I., K.-H. Kock and G. Parkes. 1996. Ovarian development associated with first maturity in three species of Antarctic channichthyid species. *J. Fish Biol.*, 49: 1019–1026.

Finney, D.J. 1978. *Statistical Method in Biological Assay*. 3rd Edition. Charles Griffin, London: 508 pp.

Kock, K.-H. and I. Everson. 1998. Age, growth and maximum size of Antarctic notothenioid fish – revisited. In: di Prisco, G., E. Pisano and A. Clarke (Eds). *Fishes of Antarctica: a Biological Overview*. Springer-Verlag, Milan: 29–40.

Kock, K.-H. and A. Kellermann. 1991. Reproduction in Antarctic notothenioid fish: a review. *Ant. Sci.*, 3 (2): 125–150.

Lane, P.W. 1993. Procedure 'FIELLER'. In: *Genstat 5 Procedure Library Manual Release 3 (1)*. Numerical Algorithms Group, Oxford: 160–162.

Livingston, M.E., M. Vignaux and K.A. Schofield. 1997. Estimating the annual proportion of non-spawning adults in New Zealand hoki, *Macruronus novaezelandiae*. *Fisheries Bulletin*, 95: 99–113.

Ni, I.-H. and E.J. Sandeman. 1984. Size at maturity for Northwest Atlantic redfishes (*Sebastes*). *Can. J. Fish. Aquat. Sci.*, 41: 1753–1762.

Payne, R.W. 1993. Procedure 'PROBITANALYSIS'. In: *Genstat 5 Procedure Library Manual Release 3 (1)*. Numerical Algorithms Group, Oxford: 267–270.

Payne, R.W., P.W. Lane, D.B. Baird, A.R. Gilmour, S.A. Harding, G.W. Morgan, D.A. Murray, R. Thompson, A.D. Todd, G. Tunnicliffe Wilson, R. Webster and S.J. Welham. 1997. *Genstat 5 Release 4.1 Command Language Manual*. Numerical Algorithms Group, Oxford: 384 pp.

SC-CAMLR. 1997. Report of the Working Group on Fish Stock Assessment. In: *Report of the Sixteenth Meeting of the Scientific Committee (SC-CAMLR-XVI)*, Annex 5. CCAMLR, Hobart, Australia: 239–425.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshwater Res.*, 41: 199–222.

Liste des tableaux

Liste des figures

Список таблиц

Список рисунков

Lista de las tablas

Tabla 3: Valores de L_{m50} e intervalos de confianza del 95% (fiduciarios) estimados de ajustes de curvas logísticas (asíntota = 1) con el método FIELLER para los peces hembra y comparaciones con las estimaciones que toman en cuenta una falta de respuesta utilizando las curvas logísticas ajustadas por el procedimiento PROBITANALYSIS (asíntota libre) de Genstat para 1997.

Lista de las figuras

Figura 1: Representación diagramática de la situación en la cual sólo un 80% de todos los peces sexualmente maduros desovaron.

Figura 2: Proporción de peces macho que liberaron esperma graficado en función de la talla. La línea ajustada está limitada por la asíntota igual a uno.

Figura 3: Proporción de peces hembra que desovaron graficado en función de la talla. La línea entrecortada está limitada por la asíntota igual a uno. La línea continua representa la curva ajustada por el procedimiento PROBITANALYSIS sin limitaciones asintóticas.