

DEPTH DISTRIBUTION AND SPAWNING PATTERN OF *DISSOSTICHUS ELEGINOIDES* AT SOUTH GEORGIA

D.J. Agnew

Renewable Resources Assessment Group
Imperial College, 8 Prince's Gardens
London SW7 1NA, United Kingdom

L. Heaps, C. Jones, A. Watson, K. Berkiet and J. Pearce

Marine Resources Assessment Group Ltd
47 Prince's Gate
London SW7 2QA, United Kingdom

Abstract

Trends in mean length and maturity stage of Patagonian toothfish (*Dissostichus eleginoides*) were examined using data from approximately 7 000 fish sampled by observers from the 1998 fishery around South Georgia and Shag Rocks (Subarea 48.3). *D. eleginoides* were distributed down the shelf slope with an approximately linear relationship existing between depth and fish length. A statistically significant pattern of changing mean length at depth with month was detected, suggesting movement of animals both up and down slope at particular times of year. Months with a high mean length at depth are May and August, and with a low mean length at depth – April and July. Examination of maturity data suggests that in addition to a major spawning event in late July/August, there may be a small spawning event in April/May. Detailed examination of maturity-at-depth data suggests that mature males move down slope and females move up slope to meet at breeding areas defined by slope position (between 800 and 1 200 m depth) and not by geographical position. Pre-spawning animals appear to be distributed all around the South Georgia and Shag Rocks shelf slopes. Spent animals of both sexes appear to move up slope to shallower water, and are concentrated to the northeast of Shag Rocks. Few spent fish were found around South Georgia. This concentration of large post-spawning fish may have some implications for the management of the fishery.

Résumé

Les tendances des longueurs moyennes et des stades de maturité de la légine australe (*Dissostichus eleginoides*) sont examinées en utilisant les données d'environ 7 000 poissons échantillonnés par des observateurs de la pêche de 1998 autour de la Géorgie du Sud et des îlots Shag (sous-zone 48.3). Sur la pente du plateau fréquenté par *D. eleginoides*, on note une relation presque linéaire entre la profondeur et la longueur des poissons. Une caractéristique importante sur le plan statistique est décelée dans le changement de la longueur moyenne en fonction de la profondeur et du mois, ce qui suggère que les poissons se déplacent tant vers le haut que vers le bas de la pente à divers moments de l'année. La longueur moyenne en profondeur est élevée en mai et août, et faible en avril et juillet. L'examen des données de maturité suggère qu'outre la principale période de frai, fin juillet/août, une ponte secondaire pourrait avoir lieu en avril/mai. L'examen approfondi des données de maturité selon la profondeur laisse entendre que les mâles matures descendent le long de la pente et que les femelles la remontent pour se rencontrer dans des secteurs de reproduction définis selon la position sur la pente (entre 800 et 1 200 m de profondeur) et non la position géographique. Les poissons en état de pré-ponte semblent être dispersés sur les accores, tout autour de la Géorgie du Sud et des îlots Shag. Après le frai, les poissons des deux sexes semblent remonter la pente vers des eaux moins profondes, et se concentrer au nord-est des îlots Shag. Très peu ont été rencontrés autour de la Géorgie du Sud. Cette concentration de poissons de grande taille ayant passé le stade du frai pourrait avoir des conséquences pour la gestion de la pêche.

Резюме

В этой статье анализируются стадии зрелости и тенденции в изменении средней длины патагонского клыкача (*Dissostichus eleginoides*) на основании данных по примерно 7000 особей, отобранных наблюдателями в 1998 г. в ходе промысла у

Южной Георгии и скал Шаг (Подрайон 48.3). Особи *D. eleginoides* были распространены вниз по склону шельфа, причем существовала примерно линейная зависимость между глубиной и длиной рыбы. Был отмечен статистически значимый характер изменения средней длины по глубинам в зависимости от месяца, что говорит о передвижении рыбы вверх и вниз по склону в зависимости от времени года. Месяцы с большой средней длиной на глубине были май и август, а с незначительной – апрель и июль. Изучение данных о половозрелости говорит о том, что в дополнение к основному периоду нереста в конце июля/августе может происходить меньший по масштабу нерест в апреле/мае. Детальный анализ данных по степени зрелости в зависимости от глубины наводит на мысль, что половозрелые самцы движутся вниз по склону, а самки – вверх по склону, чтобы встретиться в местах нереста, определенных расположением склона (между 800 и 1200 м глубины), а не географическим положением. Представляется, что преднерестовые особи распространены на всех шельфовых склонах Южной Георгии и скал Шаг. Отнерестившиеся самцы и самки перемещаются вверх по склону в более мелкие воды и концентрируются к северо-востоку от скал Шаг. У Южной Георгии было найдено очень мало отнерестившихся особей. Такое концентрированное распределение крупных посленерестовых особей может сказаться на управлении этим промыслом.

Resumen

Las tendencias en el largo promedio y en los estadios de madurez del bacalao de profundidad (*Dissostichus eleginoides*) fueron examinados utilizando los datos de unos 7 000 peces muestreados por los observadores durante la pesquería efectuada en 1998 alrededor de Georgia del Sur y de las rocas Cormorán (Subárea 48.3). El stock de *D. eleginoides* se distribuyó a lo largo de la pendiente, y se observó una relación casi lineal entre la profundidad y el largo del pez. Se detectó un patrón estadísticamente significativo de cambio en el largo promedio con la profundidad y el mes, indicando que los peces se desplazan hacia arriba y abajo en la pendiente en temporadas específicas durante el año. En mayo y agosto el largo promedio aumenta a mayor profundidad mientras que en abril y julio la relación es inversamente proporcional. Del examen de los datos de madurez se infiere que en julio/agosto ocurre un gran desove y posiblemente se da uno menor en abril/mayo. El examen detallado de los datos de madurez en función de la profundidad sugiere que los machos maduros descienden por la pendiente y las hembras se desplazan hacia arriba para juntarse en las zonas de reproducción definidas más bien por la profundidad de la pendiente (entre 800 y 1 200 m de profundidad) que por la ubicación geográfica. Los animales en estado de predesove aparentemente están distribuidos alrededor de las pendientes de las plataformas de Georgia del Sur y de las rocas Cormorán. Los animales de ambos sexos que ya han desovado parecen desplazarse hacia aguas menos profundas y se concentran al noreste de las rocas Cormorán. Se encontraron pocos peces que ya habían desovado alrededor de Georgia del Sur. Esta concentración de peces de gran tamaño en la etapa posterior al desove puede tener algunas consecuencias para la ordenación de la pesquería.

Keywords: Patagonian toothfish, *Dissostichus eleginoides*, maturity, spawning, South Georgia, Shag Rocks, depth distribution, CCAMLR

INTRODUCTION

The biology of Patagonian toothfish (*Dissostichus eleginoides*) is relatively well known. The fish are distributed on continental shelves and shelf slopes around South America and on a number of sub-Antarctic islands. In all areas fish increase in size with depth (South Georgia: Zhivov and Krivoruchko, 1990; Kerguelen: Duhamel, 1991; Chile: Moreno, 1991). Spawning is thought to take place in deep waters, with eggs rising into the upper 500 m of the water column

over the shelf slope region (Evseenko et al, 1995). Around South Georgia the spawning period is generally considered to be in the winter months, from June to September (Konfortin and Kozlov, 1992; Evseenko et al., 1995), similar to that in Chilean waters (July to August; Moreno et al., 1997) and around Kerguelen (around June; Duhamel, 1991). This differs somewhat from the data reported by de Clers et al. (1996) which indicates spawning on the eastern edge of Burdwood Bank from September to November.

Table 1: Number of fish sampled for maturity by month.

	April	May	June	July	August
South Georgia	736	844	446	1 326	212
Shag Rocks	1 021	1 153	475	366	658

The longline fishery for *D. eleginoides* is the principal finfish fishery around the South Georgia and Shag Rocks shelf. When this fishery started in 1989, fishing was conducted year round (CCAMLR, 1998). However, following concern about the incidental mortality of seabirds caught on longlines, the fishing season was restricted to the winter period when the abundance of seabirds around South Georgia is low, and when longlines may be set during the hours of darkness when seabirds are not as active as during daylight (CCAMLR, 1994, paragraph 8.27). In 1998 the season was from 1 April to 31 August.

Given that the fishery is now constrained to the time when *D. eleginoides* are known to spawn, there might be some concern that there exists potential for targeting spawning concentrations. Catches appear to be distributed on the shelf slope all around South Georgia and Shag Rocks, and so far there has been no suggestion of a massive concentration of effort in one small area. However, the fishery is developing rapidly and vessels are targeting fish of some specific size categories to meet market requirements. Detailed information on *D. eleginoides* spawning behaviour is not available. Consequently, we used data from observers in the 1998 commercial fishery to examine the distribution of *D. eleginoides* in time, space and over a wide depth range, both prior to and during the major winter spawning period.

METHODS

Data were analysed from eight UK observers on four vessels (referred to below as vessels A to D) in Subarea 48.3 in the 1998 season. The vessels were chosen to provide the most complete coverage of all areas and days fished (April to August inclusive), and together accounted for 47% of the catch of the 11 vessels that took part in the fishery. Most of the catch of these vessels each month was taken around Shag Rocks (70 to 80% of catches in April, June and August, and 55% of catches in May), except in July when 73% of the catch was taken around South Georgia. Each vessel undertook between two and three cruises to Subarea 48.3 over the fishing season, the inter-cruise time consisting of about a week's return to

port for landing the catch. Two observers were present on each vessel, one observing the first cruise and the other observing the second (and third) cruises. The choice of vessels was also influenced by the need to provide sufficient overlap between fishing periods so that Generalised Linear Models (GLMs) would be able to satisfactorily estimate the effects of various factors.

Observations were made in accordance with the CCAMLR Scheme of International Scientific Observation (CCAMLR, 1999). A sampling protocol was adopted in which samples were taken at random over the duration of line haul. The expected duration of line haul was divided into hourly or half-hourly periods, two periods being chosen at random for sampling the catch and two for recording events on deck. Some flexibility was required with this system as fishing operations were not identical on all vessels. Table 1 presents the total number of animals sampled.

Data for analyses involving depth as a parameter were limited to sets where the difference between the shallowest and deepest part of the set was ≤ 200 m. Mean depth referred to below is the mid-point of this range. Mean length of all *D. eleginoides* measured by the observer was calculated for each haul, and an array of mean length by haul, area, depth and vessel was produced. In order to produce contour plots of maturity stage by depth and time the proportion of animals of a given maturity stage (stages described in Kock and Kellermann, 1991) was calculated for half-month periods during the season for each vessel, by 250 m depth range and by area (Shag Rocks or South Georgia). Although some depth ranges and periods were represented by only a few fish, the average sample size per grouping was 33. Because individual fish length data may be collected by observers in a non-random way, the maturity data were corrected by first producing proportional maturity over the aforementioned groupings and by length, and then multiplying by the random length-frequency data to give a corrected proportion of each maturity stage. For this exercise, length bins of 5 cm were used.

The proportion in any sex and maturity group (by vessel, depth range, half-month and area) was multiplied by the average CPUE (numbers/1 000 hooks) by all four vessels in that depth range, half-month period and area to produce estimates of number density of all maturity stages. Data were treated similarly for the maps of maturity density, except that no restriction was placed on the depth range of a longline set. To increase sample size, the raw proportion data were used, and assumed to be representative over the two-month time frame. Catch, effort and maturity data were calculated for each 0.25° latitude and 0.5° longitude, and combined to give number density.

Analysis proceeded through fitting Generalised Additive Models (GAMs) and GLMs to the data in S-plus statistical software (Venables and Ripley, 1994). Mean length data were modelled using a gaussian error model and the proportion of animals of a given maturity stage was modelled using a binomial error model with a logit link function. Month, call sign and area were factors, depth was a continuous variable.

RESULTS

Length

In addition to month, vessel, depth and area, the models could have a number of secondary factors such as hook/longline type and observer. It was assumed, however, that these secondary factors would be closely linked, and difficult to distinguish from, vessel. For instance, although a linear model does identify observer as being important, it is much less significant than depth, area, month and vessel. The difficulty is that observers are never on the same vessel simultaneously. In 1998 the changeover between observers occurred on all vessels around June, so there is very little crossover for the estimation of observer effect.

The results are shown in Figure 1 and Table 2. Significant explanatory variables were mean depth, month and vessel. There is no evidence from the GAM that the relationship between mean length and depth is anything other than linear over the main fishing depths, though the relationship appears to depart slightly from linear at depths greater than 1 500 m. The GAM appears to show a regular decline in mean length in June and July but the GLM demonstrates that this is generally not significant. The decline in mean length is only significant in June. In the general

and Shag Rocks cases only the increase in mean length with depth is significant for May and August. It is clear, however, that the two peaks in May and August are general features, which implies either the arrival of large animals or the departure of small animals at all depths.

The slopes of the relationship between mean length and depth are similar for both Shag Rocks and South Georgia (Table 2) but there is a significant difference between intercepts. Fish seem to be slightly larger at Shag Rocks than at South Georgia at the same depth. Figure 2 demonstrates the relationship between month and mean depth seen in the GAM results. The smoothed line falls mostly below the fitted linear relationship in June and July. There is a substantial departure from the assumed linear form of the relationship between depth and mean length in August, when the mean length at shallow depths is greater than expected. The data for April are very noisy, which presumably masks the effect seen in the GAM.

Plots of mean length by depth and time are shown in Figure 3. For this purpose mean length was calculated for each 250 m depth range, by half-month periods, for each vessel. The increases in mean length at depth in May and August can be seen. The pattern is not quite as simple as is suggested by Table 1, however, because there are obviously differences between South Georgia and Shag Rocks. At the latter, there appear to be two movements of smaller fish down slope starting in late May and again in July in addition to the movements of larger fish to shallow waters in May and August. At South Georgia this down slope movement appears to be smaller from June onwards. These plots do mask the movements of individual fish, however, in that each point is a mean length, taken to represent the length-frequency distribution that actually exists.

Maturity

In 1998 the breeding period, as evidenced by a large increase in spent animals (maturity stage 5) in catches, was August (Figure 4). Throughout July there appeared to be an increase in the proportion of animals of maturity stage 4. There was also some indication of an early breeding period around early May. It is worth noting the very high proportion of spent females in catches in August, and the declining proportion of maturity stage 3 animals through July and August.

Table 2: Results of three linear models of mean length of fish in each haul (cm), against mean depth (m), month, area and vessel. The value, standard error and significance (*t*-test) of each coefficient is given. Only longlines set with a depth range of 200 m were used. The linear models are of the form

$$\text{mean fish length (cm)} = a + b \cdot D + c_m + d_r + e_s$$

where *a* is the intercept given in the table, *b* is the coefficient of depth, *D* is the depth in metres, *c_m* is the coefficient for the month *m*, *d_r* is the coefficient for the area *r* (if area is included as a factor in the model) and *e_s* is the coefficient for the vessel *s*. Coefficients for month 4, area South Georgia and Vessel A are zero. Thus the mean length predicted by the linear model of all areas (column 1) for fish at Shag Rocks at 1 000 m in month 5, Vessel A is $67.3294 + 0.0193 \cdot 1\ 000 + 5.5768 + 4.1182 - 0 = 96.32$ cm. This can be compared with the plots of mean length with depth given in Figure 2. An anova of the All Areas model is given at the foot of the table.

All Areas				Shag Rocks Only				South Georgia Only			
<i>n</i> = 84				<i>n</i> = 428				<i>n</i> = 298			
Coefficient	Value	SE	Pr(> <i>t</i>)	Coefficient	Value	SE	Pr(> <i>t</i>)	Coefficient	Value	SE	Pr(> <i>t</i>)
(Intercept)	67.3294	1.9606	0.0000	(Intercept)	71.7685	2.0321	0.0000	(Intercept)	65.4930	3.8108	0.0000
Depth	0.0193	0.0014	0.0000	Depth	0.0196	0.0018	0.0000	Depth	0.0200	0.0028	0.0000
Month 5	5.5768	1.2824	0.0000	Month 5	4.9889	1.7608	0.0053	Month 5	7.1142	2.2225	0.0017
Month 6	3.5919	1.4877	0.0164	Month 6	3.0442	2.0448	0.1387	Month 6	4.9317	2.3771	0.0399
Month 7	2.1483	1.2980	0.0990	Month 7	1.2835	2.5146	0.6105	Month 7	3.0235	1.8201	0.0990
Month 8	4.0064	1.4092	0.0048	Month 8	4.5649	1.7914	0.0119	Month 8	2.7669	2.6660	0.3012
Area Shag Rocks	4.1182	1.1307	0.0003	Vessel B	-1.9166	1.6919	0.2592	Vessel B	-1.8542	1.4986	0.2181
Vessel B	-1.6553	1.0502	0.1161	Vessel C	-3.8938	2.6609	0.1456	Vessel C	-1.7221	1.6798	0.3071
Vessel C	-2.4853	1.3797	0.0727	Vessel D	-5.9459	1.8952	0.0021	Vessel D	-2.6875	2.8256	0.3432
Vessel D	-5.5186	1.3430	0.0001								

ANOVA of the All Areas model					
Terms added sequentially (first to last)					
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Depth	1	11 690.17	11 690.17	240.1915	0.00000000
Month	4	1 100.06	275.02	5.6506	0.00021624
Area	1	270.97	270.97	5.5674	0.01896529
Vessel	3	867.67	289.22	5.9425	0.00060522
Residuals	288	14 017.03	48.67		

Table 3: Proportional maturity, 1998. Chi-squared probabilities showing significance of various factors in an anova of binomial Generalised Linear Models (depth fitted as a continuous variable).

		Maturity Stage				
		1	2	3	4	5
Females:						
Month	4 Df	0.3091	0.1823	0.2827	0.4328	0.0617
Depth	1	0.0022	0.7701	0.9128	0.0019	0.4552
Vessel	3	0.2131	0.0025	0.7923	0.3442	0.8133
Area	2	0.3197	0.9185	0.8780	0.5555	0.1943
Males:						
Month	4	0.4431	0.3811	0.0001	0.0107	0.0221
Depth	1	0.0031	0.9560	0.1966	0.2155	0.8625
Vessel	3	0.2193	0.5256	0.1192	0.0717	0.2994
Area	2	0.0307	0.7581	0.8993	0.6650	0.0384

A more detailed investigation of maturity reveals that depth and month are both important in determining the proportion of the population in one of various maturity stages (Table 3). Month appears to be an important factor for males but not for females. Depth is an important factor for animals of maturity stage 1; as one would expect, they are restricted to shallow depths. Depth would appear to be important for maturity stage 4 females, and area for maturity stage 5 males.

The distribution of maturity stages 3 to 5 by depth and by area is shown in Figures 5(a) and 5(b). Caution must be taken in interpreting the South Georgia data since sampling was not as intensive in this area and some of the grid is poorly filled (Figure 6).

For females at South Georgia there is a concentration of maturity stage 3 and 4 fish at about 1 200 m in May, which presumably gives rise to the small numbers of maturity stage 5 fish seen at the same time and depth. Around Shag Rocks, maturity stage 4 animals concentrate at 1 100 to 1 200 m in July and there is evidence that they move there mostly from greater depths, as well as developing from maturity stage 3 animals which are mostly around the 800 m depth in April. There is no evidence of female spawning around Shag Rocks earlier than late July (Figure 5a). In both areas, post-spawning animals are present over the whole depth range, but appear to be particularly concentrated at shallower depths.

There seem to be two major concentrations of male animals of maturity stage 4 in both areas at around 1 400 m in April/May and at 800 m in June/July (Figure 5b). Both concentrations show strong down-slope diagonals, evidence of a depth-related movement (but see the above caveat

about the sample grid). Once again post-spawning males are particularly concentrated at shallower depths, mostly around Shag Rocks (Figure 5b).

Figures 7(a) and 7(b) clearly demonstrate the uneven distribution of post-spawning animals. In these figures the number density of maturity stages is plotted by 0.25° of longitude by 0.5° of latitude. While maturity stage 5 animals are found around South Georgia, the highest densities are concentrated to the southwest of Shag Rocks in May (the high density of spent males in Figure 7a) and to the northeast of Shag Rocks in August. This is in contrast to the distribution of maturity stage 4 animals, which appear to be more evenly distributed between the two areas. Once again some caution must be exercised in drawing conclusions from these data since sampling around South Georgia, especially in August, was not very extensive. This was due to the abovementioned distribution of effort of the vessels. However, even with this low level of effort 214 fish were sampled around South Georgia, only 14 of which were maturity stage 5 females and only four were stage 5 males. Conversely, around Shag Rocks, of 659 fish sampled, 143 were maturity stage 5 females and 105 were stage 5 males. Of approximately equal numbers of fish sampled in each area over the course of the season (3 564 around South Georgia, 3 673 around Shag Rocks), 4.5% and 5.7% were female maturity stage 5 and male stage 5 respectively around Shag Rocks, but only 1.7% and 1.6% were female and male stage 5 respectively around South Georgia.

DISCUSSION

That *D. eleginoides* are distributed down the shelf slope in relation to their size is not a new

finding (Zhivov and Krivoruchko, 1990; Konforokin and Kozlov, 1992; see Moreno et al., 1997 for a review). However, the very close linear relationship shown in Figure 1 is somewhat surprising. When examined in detail (Figure 2), the strong linear relationship holds up even when there is other evidence of large movements of animals both up and down slope. The distribution of these fish is obviously very strongly controlled by depth.

Caution must be exercised when conducting examinations of distributional changes using maturity, because changes in apparent distribution may, of course, simply be a result of progression between maturity stages. Some caution must also be exercised when looking at maturity stage 3 and 4 animals, when there may be some difficulty in obtaining consistent staging by all observers on what is a subjective classification (SC-CAMLR, 1997, paragraph 3.33). However, combining data from many observers should eliminate most of this problem.

Spawning behaviour is probably variable from year to year, but in 1998 there seem to have been two spawning events. The first was in late April/May and the second, a major spawning event, in late July/August. Everson and Murray (1998) suggest that breeding in 1997 appears to have been delayed, probably taking place in August rather than late July, and without a May spawning event. Observations conducted by us in the 1998 season indicate that fish in the last stages of maturity 4, almost in a 'ripe running' condition, were found throughout August.

The picture that emerges is of a species with distinct spawning times (at least two in Subarea 48.3) and a high degree of mobility between these times. The major spawning time is late July and August. Our data suggest that *D. eleginoides* form spawning groupings at between 800 and 1 200 m depth. Zhivov and Krivoruchko (1990) suggest that animals spawn at shallower depths than this, but their sampling was by trawl and thus restricted to shallower depths, and it is also not clear whether they recorded spawning or just the presence of spent animals. The September 1997 UK trawl survey (Everson, 1997) did record some maturity stage 5 females, also at much shallower depths than the longline fishery.

Prior to spawning, animals move to the spawning depth, dispersing immediately afterwards, mostly up slope. It is well known that males mature at smaller sizes, and younger ages,

than females (first maturity for males is usually at age 4, females at age 10; Moreno, 1998). The size at 50% maturity ($L_{50\%}$) in 1998 calculated from our data was 75 cm for males and 101 cm for females. It is thus quite reasonable that, given the strong linear relationship between size and depth, mature females should be more prevalent at deeper depths than mature males (as Figure 5). Consequently, females should migrate up slope to breed, in contrast to males, which should migrate down slope. What is unexpected is the subsequent up slope movement of both sexes. This causes the rise in the mean length at depth in May and August (Figure 1), and the presence of large fish at shallow depths (Figure 2).

Late maturity (maturity stage 4) animals are found on all shelf slopes around South Georgia and Shag Rocks (Figure 7b). In 1998 high concentrations of post-spawning animals were only seen around Shag Rocks, although they were not absent from South Georgia. This distribution could have been due to delayed spawning around South Georgia in comparison to Shag Rocks, low levels of effort leading to restricted sampling around South Georgia, or movement of animals to shallow Shag Rocks areas immediately post-spawning. Although almost no sampling was possible on the northwest South Georgia shelf edge (Figure 7b), we do not believe that sampling alone was responsible for the observed effect, since, despite the low level of effort, 214 fish were examined from South Georgia in August. Without sampling in September at depth around South Georgia it is not possible to distinguish between the delayed spawning and post-spawning migration hypotheses.

There exists the possibility that spawning itself is primarily taking place at Shag Rocks, but in this case one would expect to see a progressive movement of maturity stage 4 animals from South Georgia to Shag Rocks throughout July and very high densities of pre-spawning animals there. In this study that was not observed, and it seems more likely, therefore, that spawning is taking place over most of the shelf area rather than in one particular area. *D. eleginoides* eggs have been found in waters up to 500 km beyond the continental shelf edge, to the north of South Georgia and Shag Rocks between 32° and 40°W (Evseenko et al., 1995). This suggests drift away from their spawning positions. Given the nature of the currents in this area, these eggs could have originated from either Shag Rocks or the western part of the South Georgia shelf slope, and from either the north or the south of the shelf.

If animals do form spawning or post-spawning aggregations at predictable times, then this might have management implications. It is not clear from the data presented here whether the concentration of maturity stage 5 (spent) animals at Shag Rocks, both in May and August, was the result of a spawning concentration or a post-spawning migration. What is certain is that the high densities of post-spawning fish seen in the area of 40.5–42°W and 53.25–53.75°S did produce some of the highest catch rates of the season (up to 0.5 kg/hook compared with the average for the season of about 0.25 kg/hook at Shag Rocks and 0.22 kg/hook at South Georgia) and did attract a concentration of fishing effort in the area (64% of the August catch by these four vessels was taken in that small area to the northeast of Shag Rocks). If the animals are simply post-spawning then this is likely to have very little impact on the stock. The possibility of there being areas of high concentration of animals, however, does emphasise the need to spread effort over the whole of the fishing season.

CONCLUSION

- (i) *D. eleginoides* at South Georgia and Shag Rocks are distributed down the shelf slope with an approximately linear relationship existing between depth and fish length. A statistically significant pattern of changing mean length at depth with month was detected, suggesting movement of animals both up and down slope at particular times of year.
- (ii) Examination of maturity data suggests that in addition to a major spawning event in late July/August, there may be a small spawning event in April/May.
- (iii) Detailed examination of maturity-at-depth data suggests that mature males move down slope and females move up slope to meet at breeding areas defined by slope position (between 800 and 1 200 m depth) and not by geographical position. Pre-spawning animals appear to be distributed all around the South Georgia and Shag Rocks shelf slopes. Spent animals of both sexes appear to move up slope to shallower water, and are concentrated to the northeast of Shag Rocks.

ACKNOWLEDGEMENTS

We would like to thank all the UK observers who collected the data from 1998 that we have analysed: C. Cooke, N. Ansell, J. Hoogesteger, D. Harrison, N. Maynard, K. Day and M. Johnson. The Chilean, Uruguayan and South African authorities are thanked for giving permission for the use of the vessels' catch and effort data. The CCAMLR Secretariat is acknowledged for creating and maintaining the useful CCAMLR observer database.

REFERENCES

- CCAMLR. 1994. *Report of the Thirteenth Meeting of the Commission (CCAMLR-XIII)*. CCAMLR, Hobart, Australia: 123 pp.
- CCAMLR. 1998. *Statistical Bulletin, Vol. 10 (1988–1997)*. CCAMLR, Hobart, Australia: 134 pp.
- CCAMLR. 1999. *Scheme of International Scientific Observation: Scientific Observers Manual*. CCAMLR, Hobart, Australia.
- de Clers, S., C.P. Nolan, R. Baranowski and J. Pompert. 1996. Preliminary stock assessment of Patagonian toothfish longline fishery around the Falkland Islands. *J. Fish Biol.*, 49 (A): 145–156.
- Duhamel, G. 1991. Biologie et exploitation de *Dissostichus eleginoides* autour des îles Kerguelen (Division 58.5.1). *Selected Scientific Papers, 1991 (SC-CAMLR-SSP/8)*. CCAMLR, Hobart, Australia: 85–106 (English abstract).
- Everson, I. 1997. Preliminary reports of UK fish survey: Subarea 48.3. Document WG-FSA-97/39. CCAMLR, Hobart, Australia: 6 pp.
- Everson, I. and A.W. Murray. 1999. Size at sexual maturity of Patagonian toothfish (*Dissostichus eleginoides*). *CCAMLR Science*, 6: 37–46.
- Evseenko, S.A., K.-H. Kock and M.M. Nevinsky. 1995. Early life history of the Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898 in the Atlantic sector of the Southern Ocean. *Ant. Sci.*, 7 (3): 221–226.
- Kock, K.-H. and A. Kellermann. 1991. Reproduction in Antarctic notothenioid fish: a review. *Ant. Sci.*, 3 (2): 125–150.

- Konforokin, I.N. and A.N. Kozlov. 1992. Pre-spawning and spawning biology of Patagonian toothfish, *Dissostichus eleginoides*, around South Georgia (Subarea 48.3). Document WG-FSA-92/13. CCAMLR, Hobart, Australia: 16 pp.
- Moreno, C.A. 1991. Hook selectivity in the longline fishery of *Dissostichus eleginoides* (Nototheniidae) off the Chilean coast. In: *Selected Scientific Papers, 1991 (SC-CAMLR-SSP/8)*. CCAMLR, Hobart, Australia: 107–119.
- Moreno, C.A. 1998. Do the males of *Dissostichus eleginoides* grow faster, or only mature before, females? Document WG-FSA-98/16 Rev. 1. CCAMLR, Hobart, Australia: 8 pp.
- Moreno, C.A., P.S. Rubilar y A. Zuleta. 1997. Ficha técnica del bacalao de profundidad. Document WG-FSA-97/42. CCAMLR, Hobart, Australia: 15 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.
- Venables, W.N. and B.D. Ripley. 1994. *Modern Applied Statistics with S-Plus*. Second Edition. Springer, New York: 548 pp.
- Zhivov, V.V. and V.M. Krivoruchko. 1990. On the biology of the Patagonian toothfish, *Dissostichus eleginoides* of the Antarctic part of the Atlantic. *Voprosy ikhtiologii*, 30 (7): 142–146.

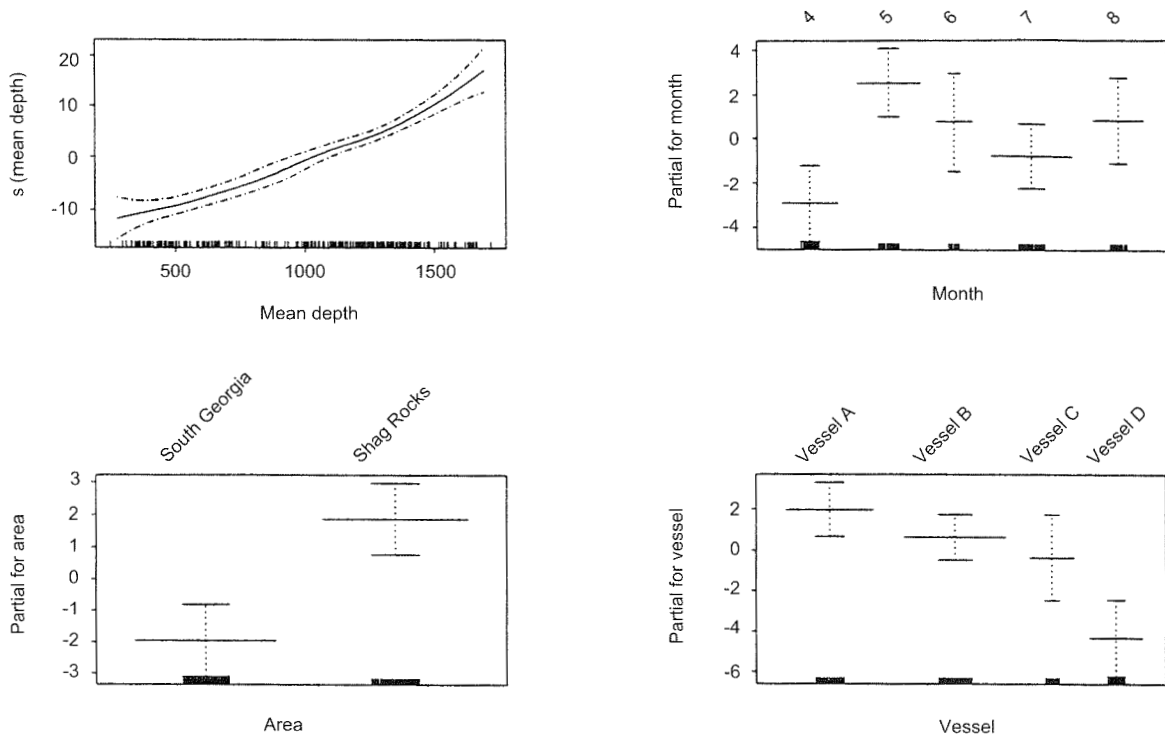


Figure 1: Generalised Additive Model functions fitted to *Dissostichus eleginoides* mean length with a spline-smoothed function of mean depth and factors for month, area and vessel: 1996 (top), 1997 (middle) and 1998 (bottom). The y-axis is the fitted function. Standard errors are plotted. Mean depth is the mid-depth of longlines, and the data were restricted to longlines set within a depth range of 200 m.

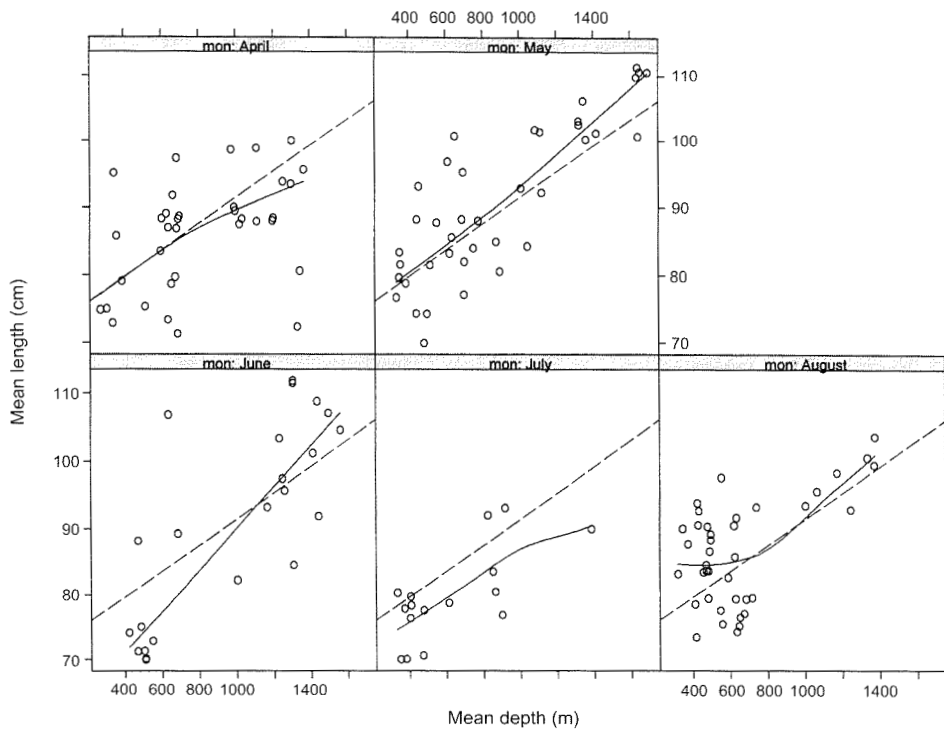


Figure 2: Plot of mean length (cm) against depth (m) for each month at Shag Rocks, with the calculated Generalised Linear Model parameters (see Table 2) as a dashed line, and a loess (locally weighted regression) smoothed fit as a solid line.

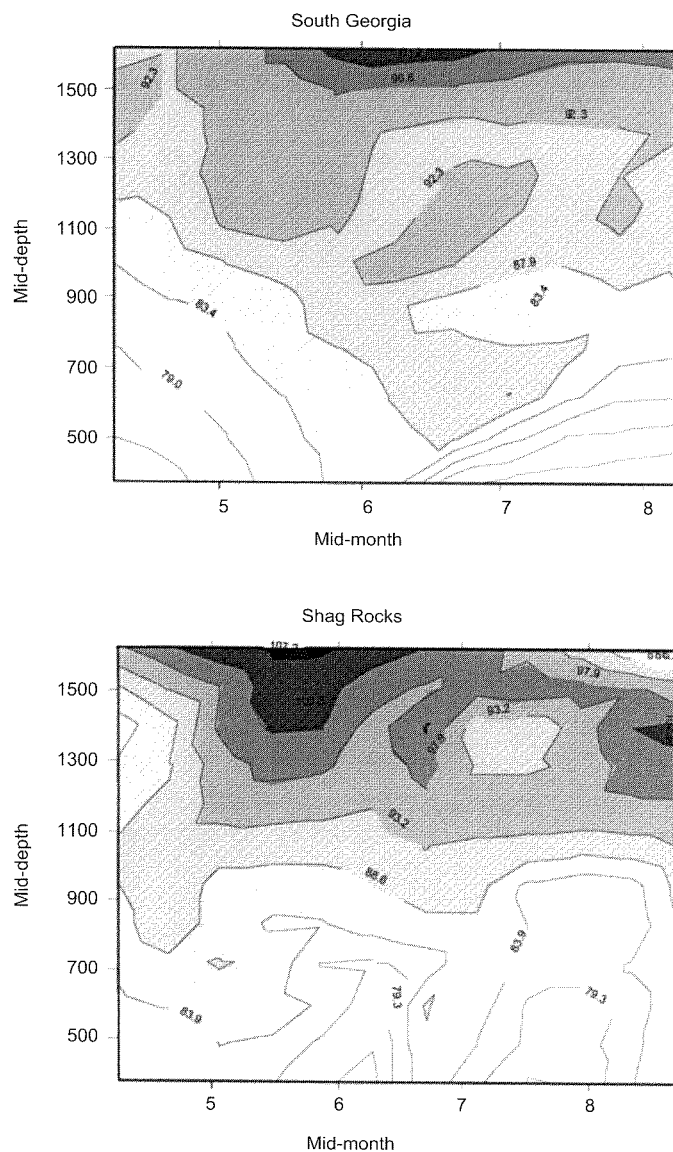


Figure 3: Contour plot of mean length of *Dissostichus eleginoides* by depth and month in 1998. On the x-axis the tic mark is the start (first) of the month, the y-axis is increasing depth (m), contours of mean length are marked in centimetres.

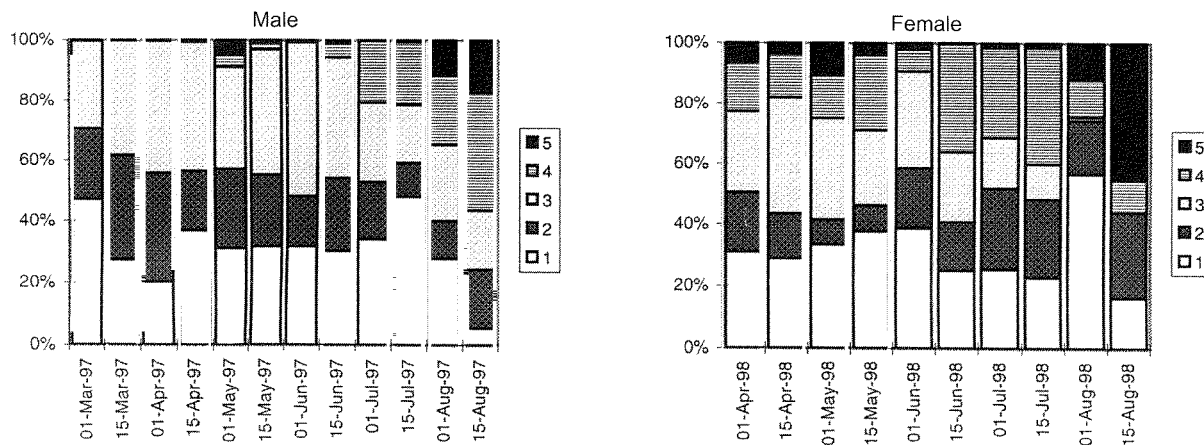


Figure 4: Proportions of animals of different maturity. Maturity stages are shown on the right.

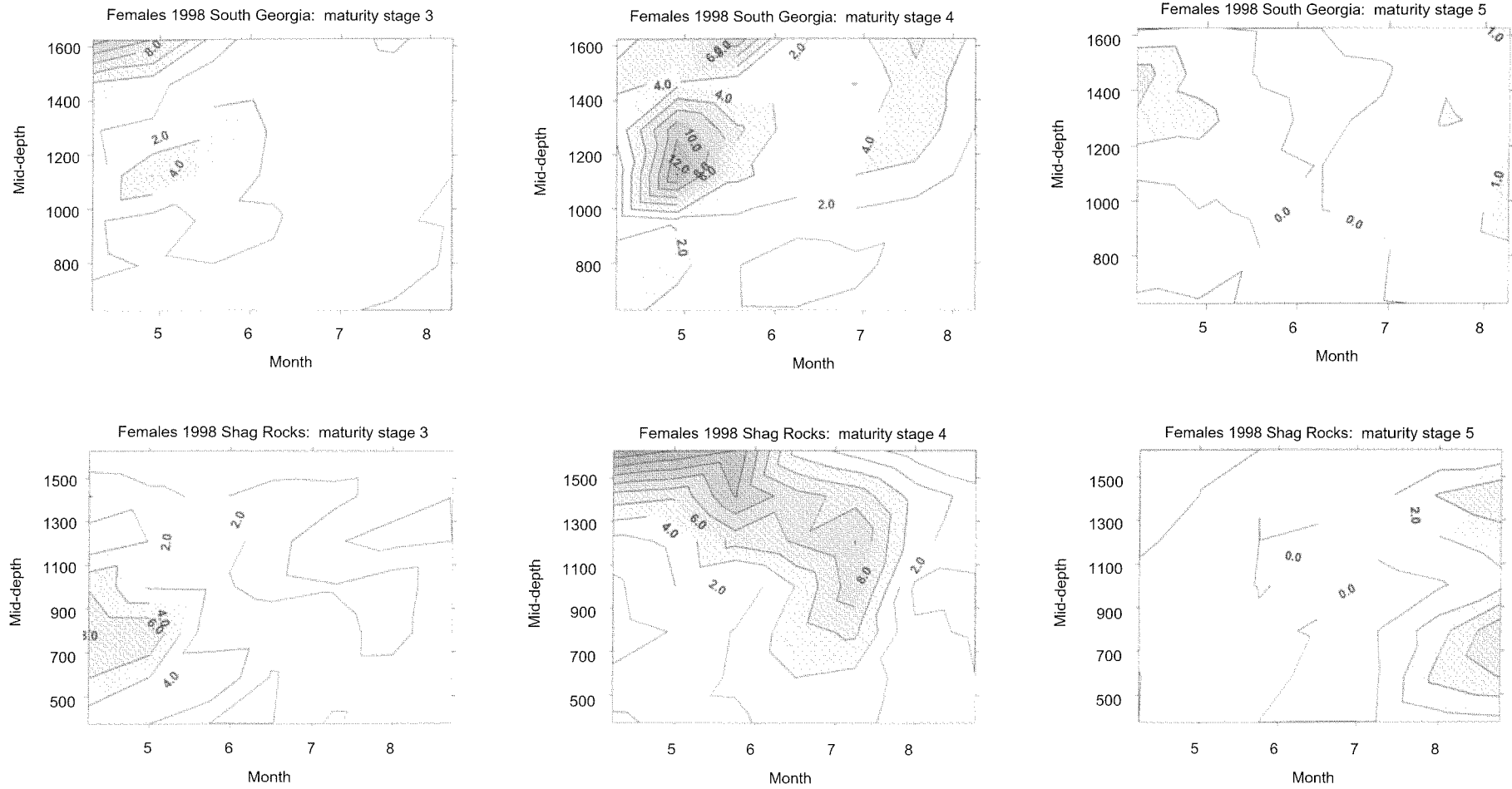


Figure 5(a): Contour plots of number density (number/1 000 hooks) of females of different maturity stages. Contours are two units apart except for South Georgia, maturity stage 5. The month labels are positioned on the first of the month.

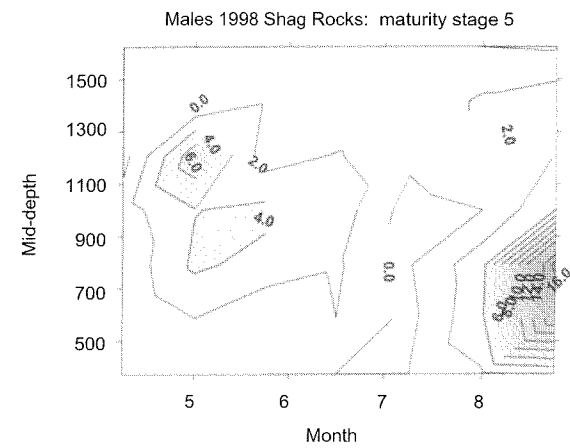
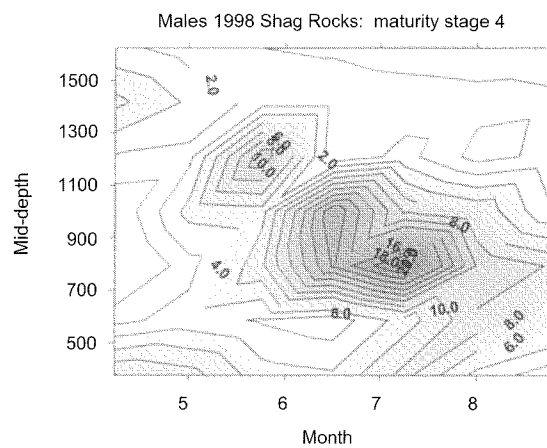
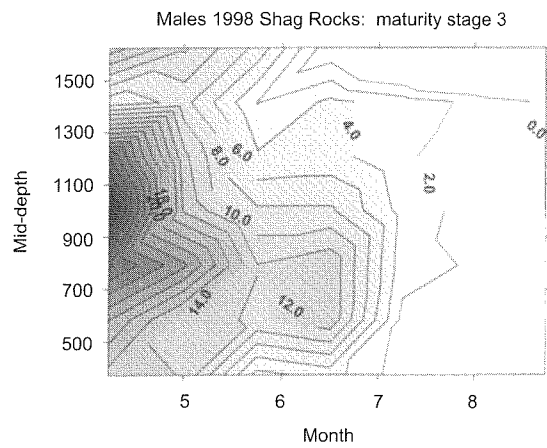
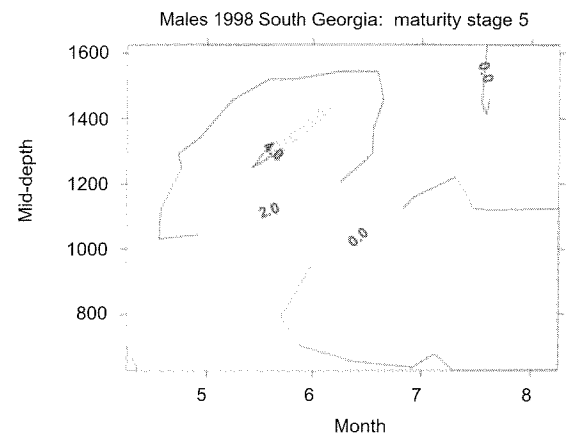
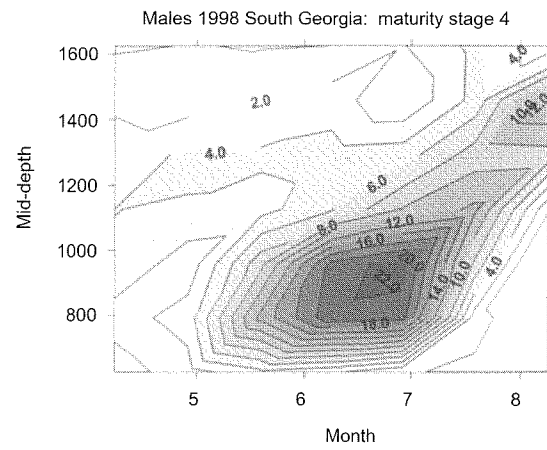
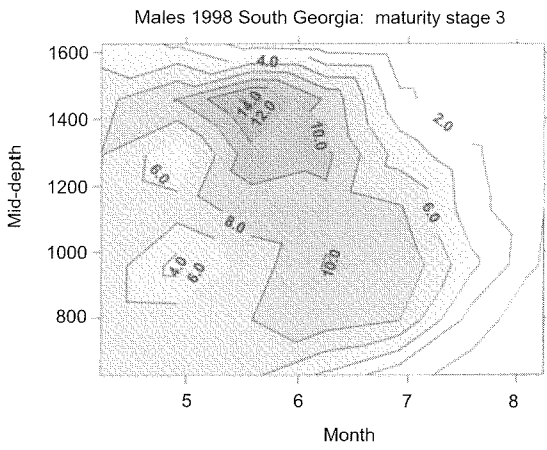


Figure 5(b): Contour plots of number density of males of different maturity stages.

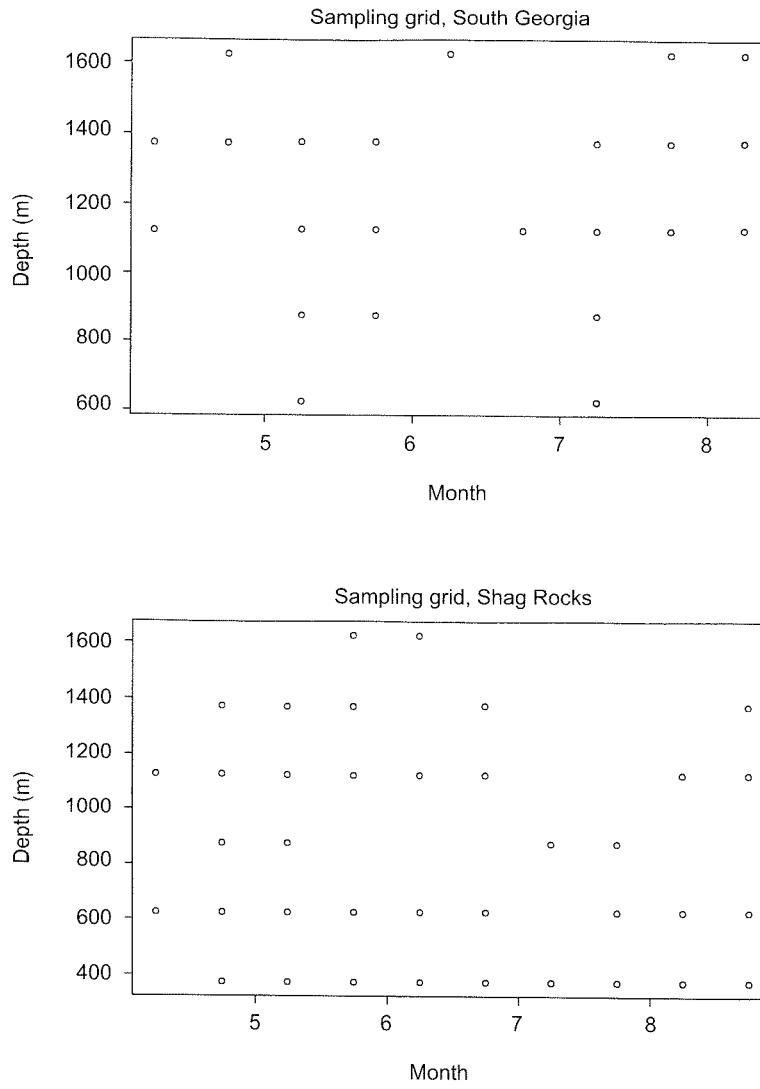
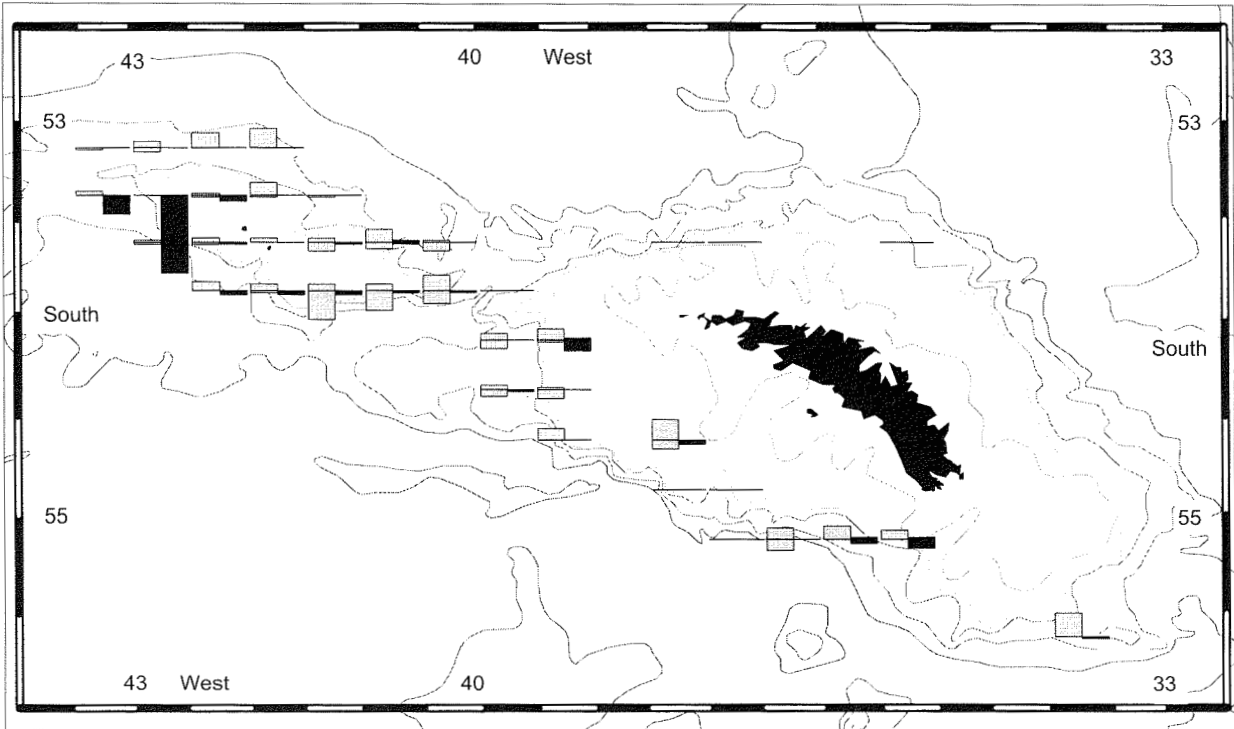


Figure 6: Sampling grids available for the production of Figure 5 contour plots.

(a)



(b)

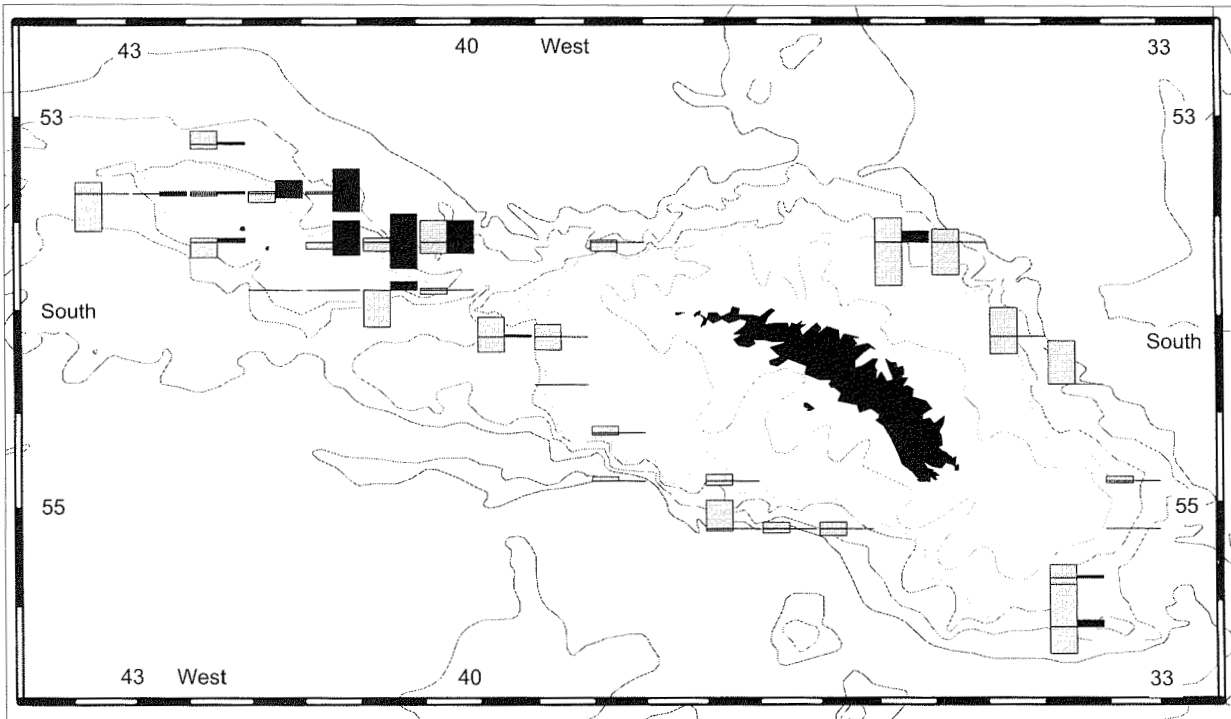
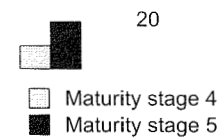


Figure 7: Number density of *Dissostichus eleginoides* maturity stages 4 and 5 in (a) May/June and (b) July/August. 100, 200, 500, 1 000 and 3 000 m depth contours are shown. At each position, bars for females extend above the horizontal line and for males, extend below it.

Number density, maturity stages 4 and 5 ($n/1\ 000$ hooks)
female (upper), male (lower)



Liste des tableaux

- Tableau 1: Nombre de poissons échantillonnés par mois en vue de déterminer le stade de maturité.
- Tableau 2: Résultats de trois modèles linéaires de la longueur moyenne des poissons dans chaque trait (cm), en fonction de la profondeur moyenne (m), du mois, du secteur et du navire. Pour chaque coefficient, la valeur, l'erreur standard et la signification (test *t*) sont donnés. Seules les poses de palangres dont l'intervalle de profondeur ne dépasse pas 200 m sont utilisées. Les modèles linéaires ont la forme suivante
- $$\text{longueur moyenne des poissons (cm)} = a + b \cdot D + c_m + d_r + e_s$$
- où *a* est le point d'intersection donné dans le tableau, *b* est le coefficient de profondeur, *D* est la profondeur en mètres, *c_m* est le coefficient du mois *m*, *d_r* est le coefficient de la région *r* (si la région est l'un des facteurs du modèle) et *e_s* est le coefficient du navire *s*. Les coefficients du mois 4, de la région de Géorgie du Sud et du navire A sont zéro. Ainsi, la longueur moyenne prévue par le modèle linéaire de toutes les régions (colonne 1) pour les poissons des îlots Shag à 1 000 m de profondeur pendant le mois 5, pour le Navire A est $67,3294 + 0,0193 \cdot 1\ 000 + 5,5768 + 4,1182 - 0 = 96,32$ cm. Ceci peut être comparé à la courbe de la longueur moyenne selon la profondeur illustrée à la figure 2. Une analyse de variance du modèle portant sur toutes les régions figure au bas du tableau.
- Tableau 3: Maturité proportionnelle, 1998. Probabilités par le test khi au carré indiquant la signification de divers facteurs dans une analyse de variance de modèles linéaires généralisés binômiaux (longueur ajustée en tant que variable continue).

Liste des figures

- Figure 1: Fonctions du modèle additif généralisé ajustées à la longueur moyenne de *D. eleginoides* avec une fonction cubique de lissage de la profondeur moyenne et les facteurs pour le mois, le secteur et le navire : 1996 (en haut), 1997 (au milieu) et 1998 (en bas). L'axe des ordonnées correspond à la fonction ajustée. Les erreurs standard sont portées sur la courbe. La profondeur moyenne est le point situé à mi-profondeur des palangres, et les données ne portent que sur les poses de palangres dont l'intervalle de profondeur ne dépasse pas 200 m.
- Figure 2: Courbe de la longueur moyenne (cm) en fonction de la profondeur (m) pour chaque mois aux îlots Shag. Les paramètres calculés du modèle linéaire généralisé (cf. tableau 2) sont représentés par des tirets, et un ajustement lissé par régression pondérée localement, par un trait plein.
- Figure 3: Courbes de niveau de la longueur moyenne de *D. eleginoides* selon la profondeur et le mois en 1998. En abscisse, l'encoche représente le début (1^{er}) du mois, l'ordonnée donne la profondeur croissante (m), les délimitations de longueurs moyennes sont marquées en centimètres.
- Figure 4: Proportions d'individus des différents stades de maturité. Ces stades sont indiqués à droite.
- Figure 5 a): Courbes de niveau de la densité en nombre (nombre/1 000 hameçons) des femelles de divers stades de maturité. Il existe une courbe toutes les deux unités, sauf en ce qui concerne le stade de maturité 5 en Géorgie du Sud. Le numéro du mois figure à l'emplacement du 1^{er} du mois.
- Figure 5 b): Courbes de niveau de la densité en nombre des mâles de divers stades de maturité.
- Figure 6: Grilles d'échantillonnage disponible pour la production des courbes de la figure 5.
- Figure 7: Densité en nombre de *Dissostichus eleginoides* des stades de maturité 4 et 5 en a) mai/juin et b) juillet/août. Les isobathes donnés correspondent à 100, 200, 500, 1 000 et 3 000 m. À chaque emplacement, les barres correspondant aux femelles dépassent au-dessus de la ligne horizontale, celles des mâles dépassent en dessous.

Список таблиц

- Таблица 1: Число рыб, выбранных для проверки степени зрелости, по месяцам.
- Таблица 2: Результаты трех линейных моделей средней длины рыбы в каждом улове (см) относительно средней глубины (м), месяца, района и судна. Приводятся значение,

стандартная ошибка и уровень значимости (критерий Стьюдента) каждого показателя. Использовались только данные по ярусам, поставленным в глубинном диапазоне 200 м. Функция в основе линейных моделей:

$$\text{средняя длина рыбы (см)} = a + b \cdot D + c_m + d_r + e_s$$

где a – приводимое в таблице значение постоянного члена, b – коэффициент глубины, D – глубина в м, c_m – коэффициент для месяца m , d_r – коэффициент для района r (если район входит как один из параметров модели) и e_s – коэффициент для судна s . Коэффициенты для месяца 4, района Южная Георгия (*South Georgia*) и судна А (*Vessel A*) равны нулю. Таким образом, полученная по линейной модели всех районов средняя длина рыбы (столбец 1) у скал Шаг на глубине 1000 м, месяц 5, судно А составляет: $67,3294 + 0,0193 \cdot 1000 + 5,5768 + 4,1182 - 0 = 96,32$ см. Можно сравнить это значение с графиками изменения средней длины по глубине (рис. 2). Дисперсионный анализ модели всех районов приводится внизу таблицы.

Таблица 3: Пропорциональная зрелость, 1998 г. Вероятности хи-квадрат показывают значимость различных факторов при дисперсионном анализе биномиальных обобщенных линейных моделей (глубина считается непрерывной переменной).

Список рисунков

- Рисунок 1: Функции обобщенной аддитивной модели, выравненные относительно средней длины *Dissostichus eleginoides* с помощью сплайновой сглаживающей функции средней длины и факторов для месяца, района и судна: 1996 (верхняя), 1997 (средняя) и 1998 (нижняя) гг. Ось у – подобранная функция. Показаны также стандартные ошибки. Средняя глубина – средняя глубина ярусов; использованы только данные для ярусов, поставленных в глубинном диапазоне 200 м.
- Рисунок 2: График средней длины (см) по глубине (м) за каждый месяц у скал Шаг; рассчитанные параметры обобщенной линейной модели (см. табл. 2) показаны пунктирной линией, сглаженная локально взвешенная регрессия (LOESS) – сплошной линией.
- Рисунок 3: Контурный график изменения средней длины *Dissostichus eleginoides* по глубине и месяцу в 1998 г. На оси х галочкой обозначено начало (первое число) каждого месяца; ось у – нарастающая глубина (м); средняя длина помечена в см.
- Рисунок 4: Доля особей в различных стадиях зрелости (стадии показаны справа).
- Рисунок 5(a): Контурные графики плотности самок (особей/1000 крючков) различной степени зрелости. Линии нанесены через две единицы, за исключением Южной Георгии, стадия зрелости 5. Название месяца соответствует первому числу этого месяца.
- Рисунок 5(b): Контурные графики плотности самцов различной степени зрелости.
- Рисунок 6: Сетка выборки, использованная для построения графиков рисунок 5.
- Рисунок 7: Плотность особей *Dissostichus eleginoides* стадий зрелости 4 и 5 в (а) мае/июне и (b) июле/августе. Показаны изобаты 100, 200, 500, 1000 и 3000 м. Часть столбцов выше горизонтальной линии относится к самкам, ниже – к самцам.

Lista de las tablas

- Tabla 1: Número de peces muestreados al mes para determinar la madurez.
- Tabla 2: Resultados de tres modelos lineales de la talla promedio de peces de cada lance (cm), en función de la profundidad promedio (m), mes, área y barco. Se da el valor, el error típico y la significación (pruebat-) de cada coeficiente. Sólo se utilizaron palangres calados en un intervalo de profundidad de 200 m. La fórmula de los modelos lineales es:

$$\text{largo promedio del pez (cm)} = a + b \cdot D + c_m + d_r + e_s$$

donde a es la intersección dada en la tabla, b es el coeficiente de profundidad, D es la profundidad en metros, c_m es el coeficiente para el mes m , d_r es el coeficiente para el área r (si se incluye el área como un factor en el modelo) y e_s es el coeficiente para el barco s . Los coeficientes para el mes 4, área de Georgia del Sur y Barco A son iguales a cero. Así, la longitud promedio predicha por el modelo lineal para todas las áreas (columna 1) para los peces de las rocas Cormorán a 1 000 m de profundidad en el mes 5, Barco A es $67,3294 + 0,0193 \cdot 1\ 000 + 5,5768 + 4,1182 - 0 = 96,32$ cm. Esto se puede comparar con los gráficos de la longitud promedio en función de la profundidad dados en la figura 2. Al pie de la tabla se presenta un análisis anova del modelo para todas las áreas.

Tabla 3: Madurez proporcional, 1998. Probabilidades del ji cuadrado que muestran la significación estadística de varios factores en un anova de modelos binomiales lineales generalizados (ajuste de la profundidad como una variable continua).

Lista de las figuras

- Figura 1: Funciones aditivas del modelo generalizado ajustadas al largo promedio de *Dissostichus eleginoides* mediante una función cúbica de la profundidad promedio y de los factores relativos al mes, área y barco: 1996 (superior), 1997 (mediana) y 1998 (inferior). El eje 'y' representa la función ajustada. Se han graficado los errores típicos. La profundidad promedio es la profundidad media de los palangres y los datos se limitaron a los palangres calados dentro de un rango de profundidad de 200 m.
- Figura 2: Gráfico de la longitud promedio (cm) en función de la profundidad (m) para cada mes en las rocas Cormorán, con los parámetros del modelo lineal generalizado representados con una línea entrecortada (ver tabla 2), y un ajuste loésico (regresión ponderada por región) como una línea continua.
- Figura 3: Gráfico de la profundidad promedio de *Dissostichus eleginoides* acotado por la profundidad y mes en 1998. En el eje 'x' el tic representa el primer día del mes, el eje 'y' muestra el aumento de la profundidad (m), los contornos de la longitud promedio se marcan en centímetros.
- Figura 4: Proporción de peces en distintos estadios de madurez. Los estadios de madurez se muestran a la derecha.
- Figura 5(a): Gráficos acotados de la densidad numérica (número/1 000 anzuelos) de hembras en distintos estados de madurez. Los contornos están separados por dos unidades excepto por Georgia del Sur, estado de madurez 5. Los meses se muestran en el primer día del mes.
- Figura 5(b): Los gráficos acotados de la densidad numérica de los machos en distintos estados de madurez.
- Figura 6: Cuadrículas de muestreo disponibles para la elaboración de los gráficos acotados de la figura 5.
- Figura 7: Densidad numérica de *Dissostichus eleginoides* en los estados de madurez 4 y 5 en (a) mayo/junio y (b) junio/agosto. Se muestran las isóbatas de 100, 200, 500, 1 000 y 3 000 m de profundidad. En cada posición la barra por sobre la línea horizontal representa a las hembras y aquella por debajo representa a los machos.