Seasonal temperature change affects the growth of the squid *Loligo gahi* (Cephalopoda: Loliginidae): I. The length-at-age relationship

Emma Hatfield[†]

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, Cambs. CB3 0ET, U.K.

[†]Current Address: National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA.
[email: ehatfiel@whsun1.wh.whoi.edu]

1

Abstract

    Loligo gahi were collected, by Scientific Observers from the Fisheries Department of the Falkland Islands Government, from bottom trawl samples caught around the Falkland Islands on both commercial and research vessels from January 1994 to November 1995. Samples were taken from both seasons of the commercial fishery in the Falkland Islands (prosecuted south of 51°20'South latitude). In addition, research samples were taken in January, June and November outside the fishing seasons, to provide individuals of a greater size range than would be present in fishery samples alone. A sub-sample of squid were taken from each sample to provide statoliths for age determination by statolith increment analysis. Sea-surface temperature data were derived for an area encompassing the southerly portion of the fishing grounds for *Loligo gahi* to provide an indicator of seasonal temperature variations for that region. Age data were derived for 486 females and 445 males. Month (or season) of hatch had a strong, significant effect on the length at age relationship of *Loligo gahi*, demonstrated by the large difference in length at age for squid hatched in the summer and winter. This study provides evidence that increased temperature during a squid's early growth period may markedly accelerate growth giving rise to significant differences in length at age for adult squid hatched at different temperatures.

Introduction

    The study of growth in cephalopods has been aided by the relatively recent discovery of growth increments in the statoliths of many species. Considerable information has been amassed on the validation of statolith increment periodicity and the relationship between squid size and age (Rodhouse and Hatfield, 1990a; Jereb et al., 1991; Jackson, 1994; Jackson et al., 1998). More recent research has enabled researchers to focus on the use of size at age information for the construction of squid

2

growth models (reviewed in Jackson, 1994), and the identification of individual cohorts through the analysis of hatch date distributions (see for example Arkhipkin, 1993; Dawe and Beck, 1997).

Growth in cephalopods has been shown to be highly variable. Much of the variability can be attributed to the plasticity of growth of these organisms, i.e., the intrinsic variability (reviewed in Jackson, 1994 ; Boyle and Boletsky, 1996). However, there is an increasing body of evidence that a large component of the variability is attributable to abiotic factors. Most studies have examined growth rates in relation to the season of year, implying a temperature effect. Forsythe (1993) predicted that even small differences in temperature (1-2°C) during the first three months of post-hatching life could create large differences in the overall adult size of a cephalopod. Broods hatching later in a given year but coinciding with higher environmental temperatures would be capable of higher growth rates, overtaking earlier broods in size, and, theoretically, of reaching greater eventual adult sizes. This phenomenon had been observed previously in *Illex argentinus* from the southern Patagonian Shelf, and attributed to temperature (Rodhouse and Hatfield, 1990b). Clearly this hypothesis offers an explanation of the poor size at age relationships seen in several cephalopod populations (Caddy, 1991). That this is not the case for some squid studied, e.g., *Illex coindetii* in NW Spain (Gonzalez et al., 1996), *Sthenoteuthis pteropus* from the central-east Atlantic (Arkhipkin and Mikheev, 1992) and *Todarodes angolensis* in the northern Benguela upwelling area (Villanueva, 1992), suggests that other abiotic factors, such as food availability, also play a crucial rôle.

Statolith growth increments have been used in the past to determine growth patterns in *Loligo gahi* (d'Orbigny) (Hatfield, 1991) and to demonstrate potential biases inherent in the measurement of growth of this species from samples taken only from the commercial fishery for the species (Hatfield and Rodhouse, 1994a). The length at age relationship in *L. gahi* from commercial samples alone is highly variable and much of this variability can probably be explained by the pattern of migration of the species through the area being fished, as the restricted depth range of the fishery tends to

catch squid of a similar size, but not a similar age. Certainly when research samples from both shallower and deeper than the range of the commercial fishery were included in the analysis, providing considerably larger and smaller squid than those caught in fishery samples, the fit to the growth model was improved (Hatfield, 1991). An additional explanation for the variability is that growth rates were determined for combined samples hatched over a number of months and that different broods of squid hatching at different times would have had different growth rates. Studies have been carried out on a number of loliginid squid species showing that the temperature at the time of hatching can make a difference to the size at age relationship, in *Loligo forbesi* from the Irish Sea (Collins et al., 1995), *Loligo pealei* from the northwest Atlantic (Brodziak and Macy, 1996), *Lolliguncula brevis* from the Gulf of Mexico (Jackson et al., 1998) and in several *Photololigo* species from Japanese waters (Natsukari et al., 1988) and from Australian waters (Jackson and Choat, 1992; Jackson, 1995).

Collection of *Loligo gahi* samples from both commercial and research vessels fishing in Falkland Islands waters in 1994 and 1995 provided the opportunity to collect sufficient numbers of statoliths to enable the effects of month or season of hatch, and therefore temperature, on growth to be examined for the first time in this species and to see if those effects could be related to the demonstrated variability in the length at age relationship for that species.

Materials and methods

Statolith Sampling. - Samples of *Loligo gahi* were taken from the commercial trawl fishery in Falkland Islands waters during the 1994 and 1995 fishing seasons (first season: February to May; second season: August to October), and from two research vessels (R/V 'Atlantida' in January 1994, M/V 'Cordella' in November 1994, June and November 1995) to provide samples from outside the restricted depth range, prescribed fishing area and seasons of the commercial fishery (see Figure 1 for catch sites of sampled squid). Commercial and research vessels deploy fine-meshed cod-

4

end nets (1.0 - 1.5 cm bar mesh) thus ensuring retention of similar size ranges of squid. These samples were collected through the Falkland Islands Government Fisheries Department (FIGFD) Observer Programme. Each sample of 150 squid was frozen aboard the vessel on which it was collected and returned to the U.K. for analysis.

Squid were dissected in the laboratory and a number of measurements taken. Refer to Macy (1982) for the full listing of measurements. These included dorsal mantle length to the nearest mm (ML), total body mass in g (BM) and sex. A representative sample of statoliths was collected from each sample of squid as follows. The ML measurements were grouped into five size classes of 30 mm each, representative of the size range sampled by the commercial and research vessels. All statoliths were sampled at random within the five size classes. For each of the first 1994 fishing season samples, statoliths were extracted from 25 females and 25 males; for each of the second 1994 fishing season samples, from 20 females and 20 males; for each of the 1995 fishing season samples from a total of 25 females and males combined.

Statolith Preparation and Increment Counts. - Statoliths were dissected out and stored in analytical grade glycerol prior to examination. Terminology and measurement of the statoliths was after Clarke (1978). Statolith preparation and examination used the method described in Arkhipkin (1995). This method grinds the statolith on both sides and counts growth increments (representing age in days) from the focus to the edge of the rostrum. Hatching dates were back-calculated.

It has not been possible to validate the one ring per day hypothesis in this species due to a number of constraints; mainly the inability to capture live adults or juveniles. However, previous age determination work on this species in relation to other research into the species' life cycle from fisheries and research samples has provided good evidence that increments are deposited at the rate of one per day (Hatfield, 1991; Hatfield and Rodhouse, 1994a, 1994b).

Linear, exponential and logarithmic models were fitted to the ML at age data to

determine the model of best fit. All transformations are natural logarithms. Statistical procedures were performed using the statistical package MINITAB v.11 (Minitab Inc., 1996).

Temperature Data. - Temperature data for 1993, 1994 and 1995 were derived from sea surface temperature (SST) data (Reynolds and Smith, 1994) for the single grid cell 52° 50' S, 59° 50' W. This area is to the south of the Falkland Islands, over depths of ~160 m, in the vicinity of the main commercial fishery for *Loligo gahi.* The SST data are from the National Oceanic and Atmospheric Administration (NOAA) operational global SST analyses. The weekly and monthly data were derived from the British Antarctic Survey marine Geographical Information System (Trathan et al., 1993).

Seasonal growth. - ML at age data were grouped by month of hatch, and by season of hatch to compare and contrast growth rates at different temperatures. The seasons were grouped as follows: spring - October, November and December; summer - January, February and March; autumn - April, May and June; winter - July, August and September. These groupings meant generally that the three warmest months (January, February and March) and the three coldest months (July, August and September) were grouped together, encompassing the two peaks of hatch seen in the back-calculated hatch data.

Results

Mantle Length at Age. - The ML at age plots for all data combined are shown in Figure 2. Linear, exponential and logarithmic curves were fitted to the data for females and males separately and the results are shown in Table 1. Each regression was significant but there was poor correlation for each model for each sex. Examination of the residuals showed the linear model to be least preferable to describe growth. As the pattern of residuals was essentially the same for the exponential and logarithmic

6

models and the difference between the adjusted r^2 was only 1% for females and 2% for males the exponential model was selected. Other growth studies on *Loligo gahi* have described growth by this model and for consistency the model is retained in this study.

The age range for females was 123 - 366 days, and for males was 132 - 339 days. The range of ML examined was 64 - 244 mm for females and 55 - 300 mm for males.

There is clearly much variation in length at age when all data are combined in the model. To assess potential sources of variability the data were grouped by month of hatch and re-examined. Analysis of covariance (ANCOVA) was performed to test for differences in growth of squid grouped in this way.

Hatchdate distribution. - The back-calculated distributions of hatchdates for female and male *Loligo gahi* are shown in Figure 3(a). The same distribution broken down by season of catch for females and males separately is shown in Figure 3(b). There were two peaks of hatch per year during the period 1993 to 1995, a major peak in July and August with a smaller peak in January and February. Squid caught in season 1 had a hatchdate distribution ranging from April to December with the peak in August (1994 capture) and July (1995 capture); those caught in season 2 had a hatchdate distribution ranging from October to June with the peak in January and February (for both 1994 and 1995 capture).

Sea Surface Temperature (SST) Data. - The mean monthly SST distribution and the calculated temperature anomalies (relative to the average monthly temperatures, or climatology data, for the period November 1981 to July 1997) for each month in the years 1993 - 1995 are shown in Figures 4 (a) and (b) respectively. Highest temperatures were observed in January, February and March, lowest temperatures in August and September. The anomaly data show that within the three year period 1993 was the warmest year overall; the summer and early autumn of 1994 were colder than average as were the winter and spring of 1995.

Temperature effects -To assess the potential effect of temperature on growth the relationship between mean ML at capture and date of hatch was examined and compared to the weekly SST data for the same period. Figure 5 shows the mean ML data for squid caught in 1994 only, as there were more age data available from that year. There is a clear trend with squid caught at a smaller size tending to be those hatched at cooler temperatures.

To examine this relationship in greater detail the length at age data were first examined to look for variations in growth rate with the data grouped by month of hatch. Table 2 shows the initial design of the ANCOVA to test for homogeneity of slopes. In the females there was significant interaction between month and age overall ($p < 0.001$) suggesting that the slopes for length at age in each month were not homogeneous, but when each month was examined separately the interactions between factor (month) and covariate (age) were only significant for the months of February, April and May ($p < 0.05$). In all other months for females the hypothesis of homogeneity of slopes was accepted and further analysis performed. In males, however, the interactions between the factors (month) and covariate (age) were not significant ($p > 0.001$) so the slopes for length at age were assumed to be homogeneous for each month of hatch. The final design of the ANCOVA is shown in Table 3. In both females and males the month of hatch significantly influenced the length at age relationship ($p < 0.001$). Figure 6a shows the adjusted mean ML for females (at age 202 days) and males (at age 213 days) for each month of hatch for which data are available, with mean monthly SST data plotted on the same graph. The relationship of mean ML per month of hatch resembles closely the trends in mean monthly SST, with the squid hatched in the summer, i.e., at higher temperatures, being significantly larger than squid of the same age but hatched in the winter months.

The length at age data grouped by hatch month were combined into season of hatch and ANCOVA performed on these seasonal data. The range of ML examined for squid grouped by season for females was - spring: 75 - 163 mm; summer: 99 - 191 mm; autumn: 64 - 244; winter: 75 - 202 mm and for males was - spring: 73 - 243 mm;

8

summer: 95 - 271 mm; autumn: 55 - 275 mm; winter: 74 - 300 mm. The combining of these data allowed a statistically more rigorous ANCOVA to be performed than was possible with the monthly hatch data. Larger sample sizes were produced, with a greater spread of age data. Thus data for each season could be compared within the same age range, which was not possible in the analyses of month of hatch. The restricted age range for females was 150 - 278 days (actual ranges - spring:123 - 278; summer: 150 - 294; autumn: 148 - 366; winter: 137 - 289) and for males 154 - 288 days (actual ranges - spring: 132 - 342; summer: 150 - 288; autumn: 154 - 339; winter: 140 - 300). Table 4 shows the initial design of the ANCOVA to test for homogeneity of slopes. In females and males the interactions between the factors (season) and covariate (age) were not significant (p>0.001) so the slopes for length at age were assumed to be homogeneous for each season of hatch. The final design of the ANCOVA is shown in Table 5. In both females and males the season of hatch significantly influenced the length at age relationship (p<0.001). Figure 6b shows the adjusted mean ML for females (at age 204 days) and males (at age 213 days) for each season of hatch for the restricted age range, with mean monthly SST data plotted on the same graph. The relationship of mean ML per season of hatch resembles closely the trends in mean monthly SST grouped by season, showing the same trend as the data when grouped by month of hatch.

Discussion

This study enabled one of the potential sources of variability in the length at age relationship to be examined in *Loligo gahi*. The low correlations in the length at age data in this study using increment counts from the statolith rostrum are comparable to data obtained from counts from the statolith dome (Hatfield, 1991; Hatfield and Rodhouse, 1994a). This variability is as a result of the high degree of plasticity in individual growth rates and seems to be an inherent feature in the analysis of squid growth (Caddy, 1991; Jackson, 1994; Boyle and Boletsky, 1996). Age data enabled hatch dates for the population to be calculated for the years 1994 and 1995 from both

commercial and research samples which in turn enabled a detailed analysis of growth rates grouped by month and season of hatch to be performed.

The seasonal component of growth was clearly quite marked in *Loligo gahi* in the relationship between mean ML at capture and date of hatch from data for 1994 and from the ANCOVA results. Squid hatched in the summer months showed a significantly larger length at age than those hatched in winter. The length at age relationship was lower for squid hatched in the spring than in the autumn even though the spring hatched squid likely encountered increasing water temperatures and autumn hatched squid likely encountered decreasing temperatures. However, in autumn the average water temperature was higher than in the spring so these squid exhibited faster early growth rates in the warmer waters. Thus there is a clear seasonal component to the growth of *L. gahi* in Falkland Islands waters.

This study supports Forsythe's (1993) hypothesis in which, using growth models based on the laboratory growth of *Loligo forbesi*, it was proposed that even a slight increase in temperature during a squid's early rapid growth phase (first 100 days) could greatly accelerate growth and significantly reduce the time required to reach adult sizes. He described growth in two phases, the exponential phase, corresponding to the time in which squid growth would be most affected by temperature (the early, rapid growth phase), followed by logarithmic growth for the rest of the life cycle where higher temperatures may produce higher growth rates but the increases would be far less dramatic. Squid in this study are clearly beyond the first rapid phase of growth. Growth in this study has been described using an exponential model, nonetheless the logarithmic model gave as good a fit to the data. The growth rates for adult squid in this study were not significantly different from each other over the age range analysed. However, the length for a given age was greater for squid hatched in warmer temperatures. Clearly then the growth rates in the early, exponential phase of growth must have differed, giving rise to a significant length difference between summer and winter hatched squid of 26 mm at age 204 days for females and 31 mm at age 213 days for males. The temperatures used in this study, taken from the National Oceanic and

Atmospheric Administration (NOAA) operational global SST analyses, may not reflect the actual temperatures experienced by hatching *Loligo gahi* in Falkland Islands waters. Temperature data taken by the Fisheries Department of the Falkland Islands Government (FIGFD) at about 2 m water depth in 1995 show a greater seasonal variation than that provided by the SST data, for 1993 -1995, in this study. The SST average annual range is approximately 5.5 - 9.5° Celsius. The shallow temperature recorder data vary from approximately 1.5 - 13° Celsius (Conor Nolan, FIGFD, pers. comm.). The spawning grounds for this species are still unknown but they are presumed to be in inshore Falkland Islands waters (Hatfield et al., 1990). Similarly, little information is available on either the distribution and/or abundance of *L. gahi* juveniles in Falkland Islands waters, or the water structure therein. Two research surveys in the austral spring of 1991 and 1992 gave different results (Hatfield and Rodhouse, 1994b). In 1991, where the near-bottom water temperatures measured by acoustic net monitor at 30 m, 65 m and 100 m differed significantly, with cooler temperatures below 30 m, most juvenile squid (presumed to be 2-3 months old) were caught at 30 m depth. In 1992 where there was no significant temperature difference with water depth (100 m depth not sampled) more juvenile squid were caught at 65 m than at 30 m depth. The SST data used in this study show very similar values of water temperature for October and November 1991 and 1992 to those temperatures at which most squid were caught (i.e., mean near-bottom temperature measured by acoustic net monitor). Thus even though the SST data are for an area of water depth of ~160 m water depth they may be indicative of the general temperature conditions in which juvenile squid can be found, at least in the austral spring.

A further model (Grist and des Clers, in press) extended Forsythe's (1993) model to the more general situation in which seawater temperature variation is sinusoidal and squid eggs may hatch continuously throughout the year, which is the case for *Loligo gahi* (see Figure 3). The model gave similar results to that of Forsythe (1993) and showed that seasonally fluctuating temperatures could directly affect the size distribution of squid over the year with younger individuals having the potential to

11

surpass the size of older individuals as in this study on L. gahi. The model also predicted that the population would rapidly separate to produce a low number of tightly synchronised cohorts each year. Two peaks of hatch are seen in this study of age data which would suggest two cohorts per year. However, other data have suggested that the population frequently may comprise up to three cohorts per year (Hatfield and Rodhouse, 1994b; Hatfield, 1996).

In loliginid squid generally, there seems to be a strong seasonal component to growth although most studies have combined data for squid hatched in the warmer vs. the colder season. However for loliginid squid in both temperate and tropical waters, the pronounced effect is similar (in *Loligo forbesi* from the Irish Sea (Collins et al., 1995), *Loligo pealei* from the northwest Atlantic (Brodziak and Macy, 1996), *Lolliguncula brevis* from the Gulf of Mexico (Jackson et al., 1998) and in several *Photololigo* species from Japanese waters (Natsukari et al., 1988) and from Australian waters (Jackson and Choat, 1992; Jackson, 1995).

Temperature is clearly an important variable in the life history of *Loligo gahi* in Falkland Islands waters. The temperature experienced by a hatchling squid in the early life cycle not only affects the rate at which its adult size is reached but may predict the size of a squid entering the fishery as a function of sea-water temperature approximately six months previously, and may ultimately determine the number of cohorts produced within the population each year (Grist and des Clers, in press). The essential information required for a complete understanding of its effect on the life cycle of L. gahi is a solid understanding of the movements of the L. gahi population over the course of a year and the annual temperature patterns in these areas.

Acknowledgements

12

paper would not have been possible without it. Alistair Murray gave much useful statistical advice. Research at the British Antarctic Survey on commercially exploited cephalopods around the Falkland Islands is funded by the Falkland Islands Government.

Literature cited

Arkhipkin A. 1993. Age, growth, stock structure and migratory rate of pre-spawning short-finned squid *Illex argentinus* based on statolith ageing investigations. Fish. Res., 16: 313-338

Arkhipkin A. 1995. Age, growth and maturation of the European squid *Loligo vulgaris* (Myopsida, Loliginidae) on the west Saharan shelf. J. mar. biol. Ass. U.K., 75: 593-604

Arkhipkin A, Mikheev A. 1992. Age and growth of the squid *Sthenoteuthis pteropus* (Oegopsida: Ommastrephidae) from the central-east Atlantic. J. Exp. Mar. Biol. Ecol., 163: 261-276

Boyle PR, von Boletsky S. 1996. Cephalopod populations: definitions and dynamics. pp. 985-1002 in: Clarke, MR (ed). The role of cephalopods in the world's oceans. Phil. Trans. Roy. Soc., Ser. B., 351(1343): 979-1112

Brodziak JKT, Macy WK. 1996. Growth of the long-finned squid, *Loligo pealei*, in the northwest Atlantic. Fish. Bull., 94: 212-236

Caddy JF. 1991. Daily rings on squid statoliths: an opportunity to test standard population models? In: Squid age determination using statoliths. Jereb PS, Ragonese S, von Boletsky S (eds). Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9-14 October 1989. N.T.R.-I.T.P.P. Special Publications, No. 1, pp 53-66.

Clarke MR. 1978. The cephalopod statolith an introduction to its form. J. mar. biol. Ass. U.K., 58: 701-712

Collins MA, Burnell GM, Rodhouse PG. 1995. Age and growth of the squid *Loligo* *forbesi* (Cephalopoda: Loliginidae) in Irish waters. J. mar. biol. Ass. U.K., 75: 605-620

Dawe EG, Beck PC. 1997. Population structure, growth and sexual maturation of short-finned squid (*Illex illecebrosus*) at Newfoundland. Can. J. Fish. Aquat. Sci., 54: 137-146

Forsythe JW. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In: Recent advances in fisheries biology. Okutani T, O'Dor RK, Kubodera T (eds). Tokai University Press, Tokyo pp 133-143

Forsythe JW, Heukelem WF. 1987. Growth. In: Cephalopod Life Cycles, Vol. II. Boyle PR (ed). Acad.Press Inc. (London) Ltd. pp 135-156

Gonzalez AF, Castro BG, Guerra A. 1996. Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. ICES J. mar. Sci., 53: 802-810

Grist EPM, des Clers S. In press. How seasonal temperature variations may influence the structure of annual squid populations. J. Math. Appl. Med. Biol.

Hatfield EMC. 1991. Post-recruit growth of the Patagonian squid *Loligo gahi* (d'Orbigny). Bull. Mar. Sci., 49: 349-361

Hatfield EMC. 1996. Towards resolving multiple recruitment into loliginid fisheries: *Loligo gahi* in the Falkland Islands fishery. ICES J. mar. Sci., 53: 565-575

Hatfield EMC, Rodhouse PG. 1994a. Migration as a source of bias in the measurement of cephalopod growth. Antarct. Sci., 6: 179-184

Hatfield EMC, Rodhouse PG. 1994b. Distribution and abundance of juvenile *Loligo gahi* in Falkland island waters. Mar. Biol., 121: 267-272

Hatfield EMC, Rodhouse PG, Porebski J. 1990. Demography and distribution of the Patagonian squid (*Loligo gahi*, d'Orbigny) during the austral winter. J. Cons. int. Explor. Mer, 46: 306-312

Jackson GD. 1994. Application and future potential of statolith increment analysis in squids and sepioids. Can. J. Fish. Aquat. Sci., 51: 2612-2625

Jackson GD. 1995. Seasonal influences on statolith growth in the tropical near shore loliginid squid *Loligo chinensis* (Cephalopoda: Loliginidae) off Townsville, North Queensland, Australia. Fish. Bull., 93: 749-752

Jackson GD, Choat JH. 1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. Can. J. Fish. Aquat. Sci., 49: 218-228

Jackson GD, Forsythe JW, Hixon RF, Hanlon RT. 1998. Age, growth and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the Northwestern Gulf of Mexico with a comparison of length-frequency versus statolith age analysis. Can. J. Fish. Aquat. Sci., 54: 2907-2919

Jereb PS, Ragonese S, von Boletsky S. 1991. Squid age determination using statoliths. Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9-14 October 1989. N.T.R.-I.T.P.P. Special Publications, No. 1: 128pp

Macy WK. 1982. Development and application of an objective method for classifying long-finned squid, *Loligo pealei*, into sexual maturity stages. Fish. Bull., 80: 449-459

Minitab Inc. 1996 MINITAB® Reference Manual, State College, PA

Natsukari Y, Nakanose T, Oda K. 1988. Age and growth of loliginid squid *Photololigo edulis* (Hoyle, 1885). J. Exp. Mar. Biol. Ecol., 116: 177-190

Reynolds RW, Smith TM. 1994. Improved global sea surface temperature analyses using optimum interpolation. J. Clim. Res., 7: 929-948.

Rodhouse PG, Hatfield EMC. 1990a. Age determination in squid using statolith growth increments. Fish. Res. 8: 323-334

Rodhouse PG, Hatfield EMC. 1990b. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). Phil. Trans. Roy. Soc. Lond. B, 329: 229-241

Trathan PN, Murphy EJ, Symon CJ, Rodhouse PG. 1993. Ecological and oceanographic relationships in the Southern Ocean. GIS Europe. 2: 135-143

Villanueva R. 1992. Interannual growth differences in the oceanic squid *Todarodes angolensis* Adam in the northern Benguela upwelling system, based on statolith growth increment analysis. J. Exp. Mar. Biol. Ecol., 159: 157-177

Table 1. *Loligo gahi.* Intercepts (A) and slopes (b) +SD for the relationship mantle length (ML) at age to find the model which best describes the data. Linear model: ML = A + b age; exponential model: lnML = A + b age; logarithmic model: lnML = A + b lnage.

	A	b	r2(adj)	N	p
linear model					
females	31.4	0.447	0.37	486	0.000
males	2.73	0.598	0.38	445	0.000
exponential model					
females	4.03	0.00371	0.39	486	0.000
males	3.91	0.00432	0.41	445	0.000
logarithmic model					
females	0.735	0.764	0.40	486	0.000
males	-0.253	0.951	0.43	486	0.000

Table 2. *Loligo gahi.* Preliminary design of ANCOVA, for testing homogeneity of slopes. In each case age is the covariate, the dependent variable is mantle length. Month is the factor (1-12).

	Females			Males		
	df	F	p	df	F	p
age	1,486	117.89	0.000	1,445	0.45	0.502
month	11,486	4.59	0.000	11,445	1.58	0.102
month x age	11,486	3.15	0.000	11,445	1.46	0.146

Table 3. *Loligo gahi.* Final design of ANCOVA. In each case age is the covariate and mantle length the dependent variable. Month is the factor (1-12). For females months 2, 4 and 5 were excluded as the slopes in these months were not homogeneous. All months were tested in the case of the males.

	Females			Males		
	df	F	p	df	F	p
age	1,393	327.77	0.000	1,445	325.21	0.000
month	8,393	18.02	0.000	11,455	12.75	0.000

Table 4. *Loligo gahi*. Preliminary design of ANCOVA, for testing homogeneity of slopes. In each case age is the covariate, the dependent variable is mantle length. Tested on the data set restricted to the ages 150 - 244 in females and 154 - 288 in males. Season is the factor (1-4), where season 1 is spring, 2 is summer, 3 is autumn and 4 is winter.

	Females			Males		
	df	F	p	df	F	p
age	1, 431	119.74	0.000	1, 441	194.34	0.000
season	3, 431	9.58	0.000	3, 441	2.80	0.040
season x age	3, 431	4.78	0.003	3, 441	1.24	0.294

Table 5. *Loligo gahi*. Final design of ANCOVA. In each case age is the covariate, the dependent variable is mantle length. Tested on the same restricted data set as in Table 4.

	Females			Males		
	df	F	p	df	F	p
age	1, 431	177.00	0.000	1, 441	308.71	0.000
season	3, 431	51.90	0.000	3, 441	44.17	0.000
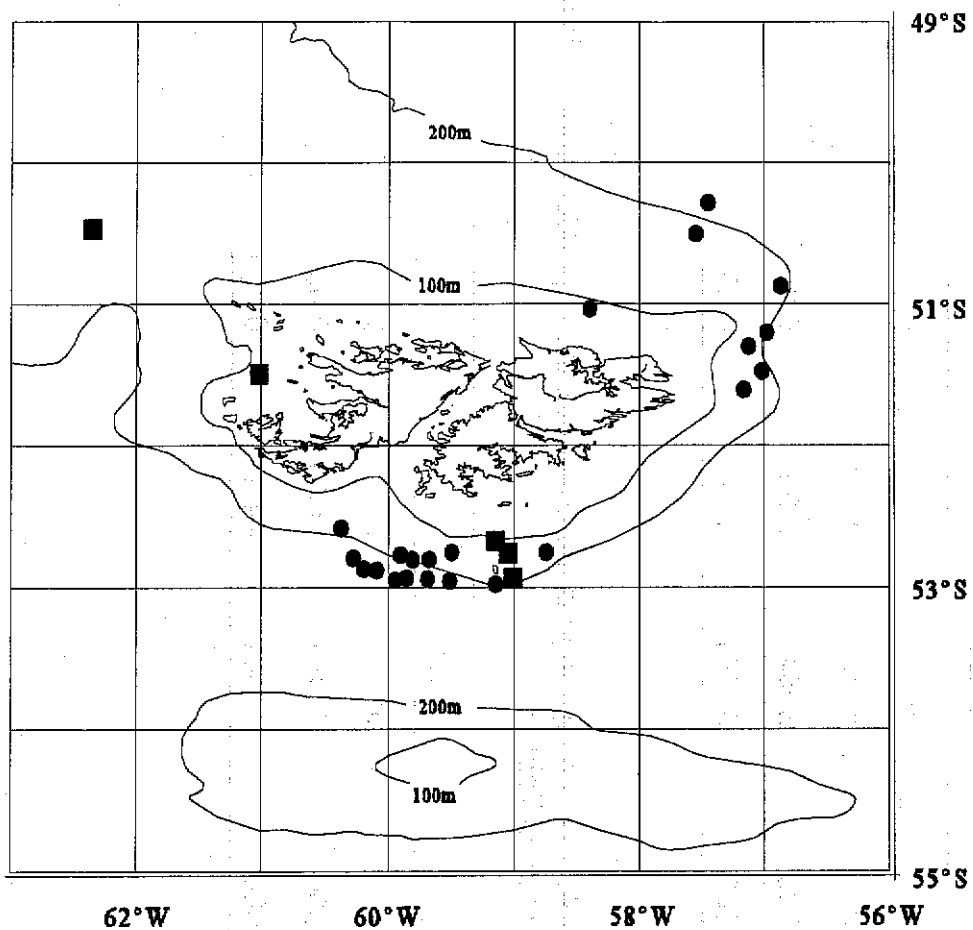
Figure 1. *Loligo gahi.* Catch sites for specimens collected in Falkland Islands waters, from both commercial and research vessels during 1994 and 1995. Circles represent commercial catches, squares represent research vessel catches.
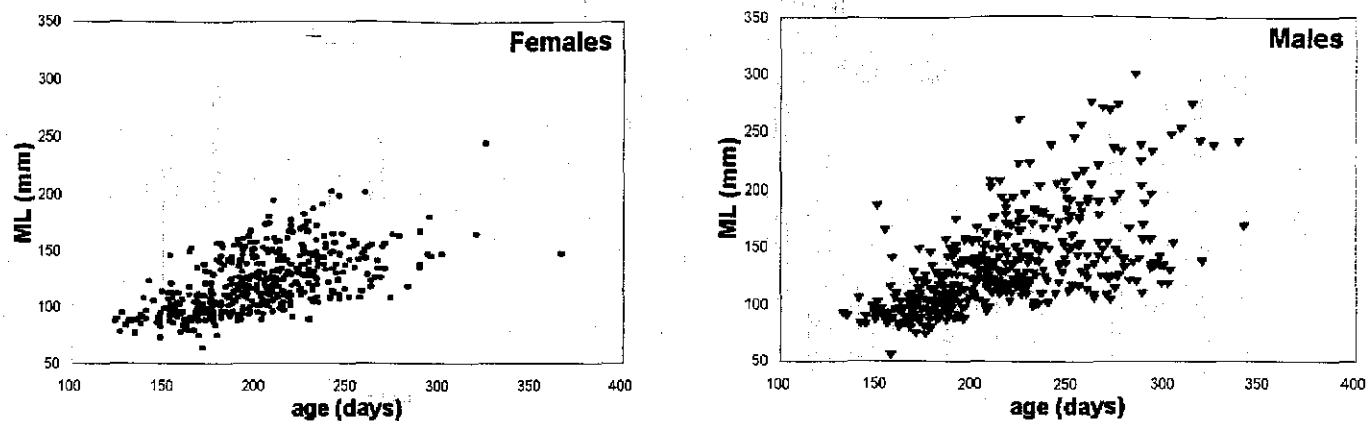
Figure 2. *Loligo gahi.* Relationship between the number of daily growth increments in the statolith (age) and mantle length.
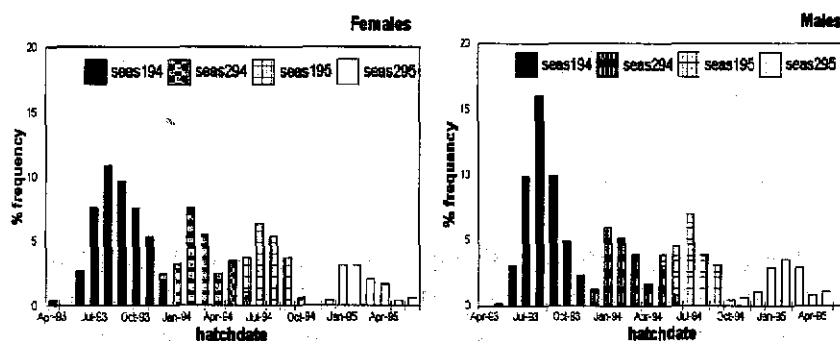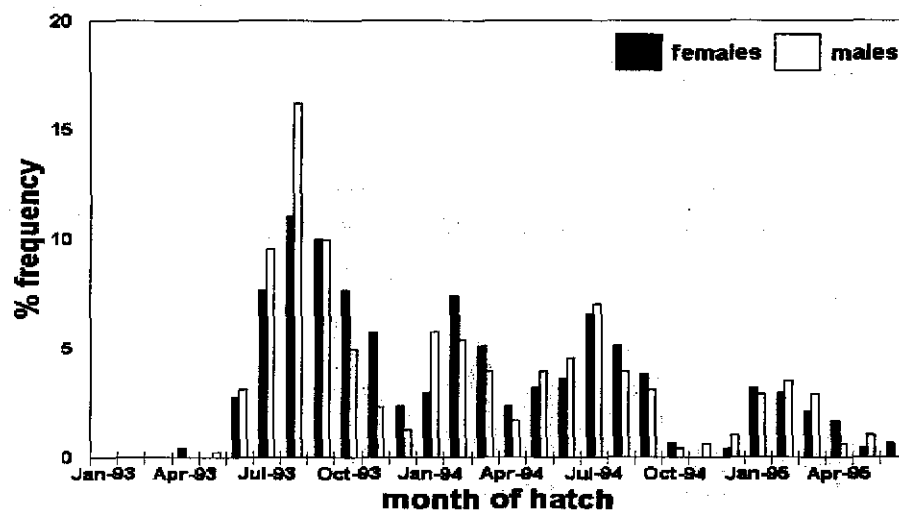

Figure 3. *Loligo gahi.* (a) Hatch date distributions calculated from known age and date of capture; (b) distributions shown for each season of capture.
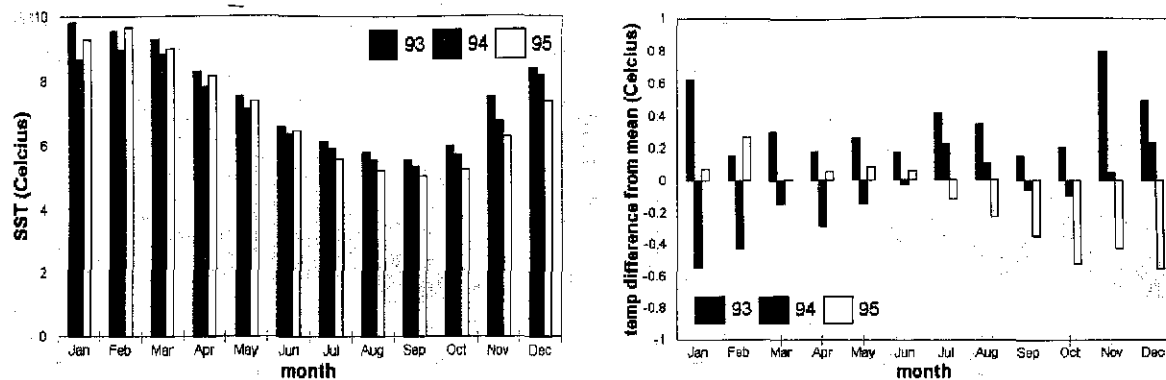
Figure 4. *Loligo gahi.* (a) Sea surface temperature (SST) distribution derived for the single grid cell 52° 50'S, 59° 50'W for the years 1993 - 1995; (b) SST anomaly data for the years 1993 - 1995, relative to the mean monthly SST data for the period November 1981 - July 1997.
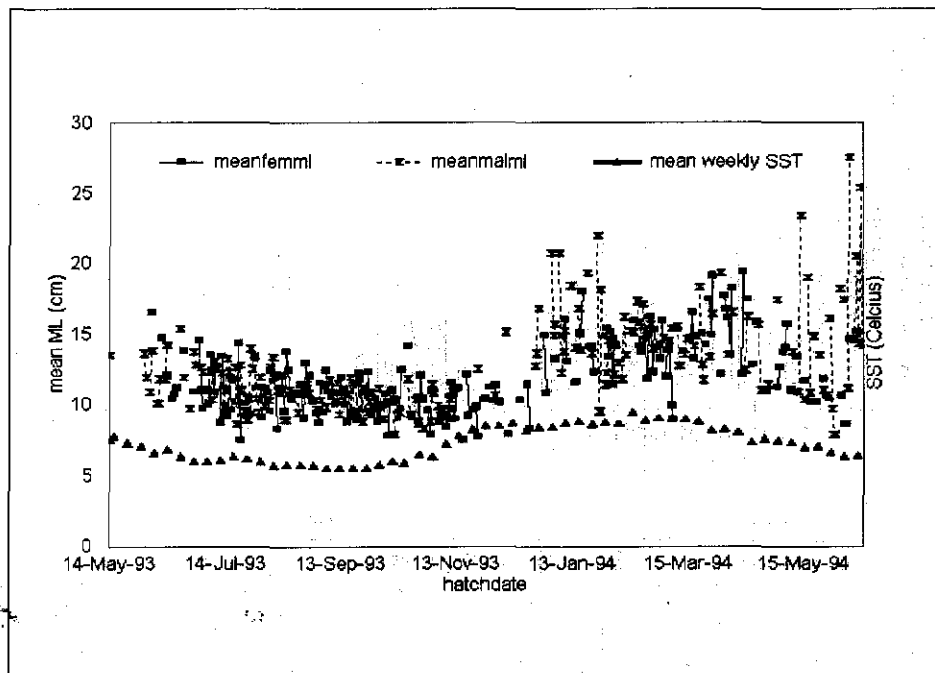

Figure 5. *Loligo gahi.* Relationship between the dorsal mantle length (ML) at capture, hatchdate, and weekly SST data for squid caught in 1994. ML values are the mean values calculated for each hatchdate. SST values show the water temperatures at the time of hatching of those squid, and demonstrate the effects of temperature on growth.
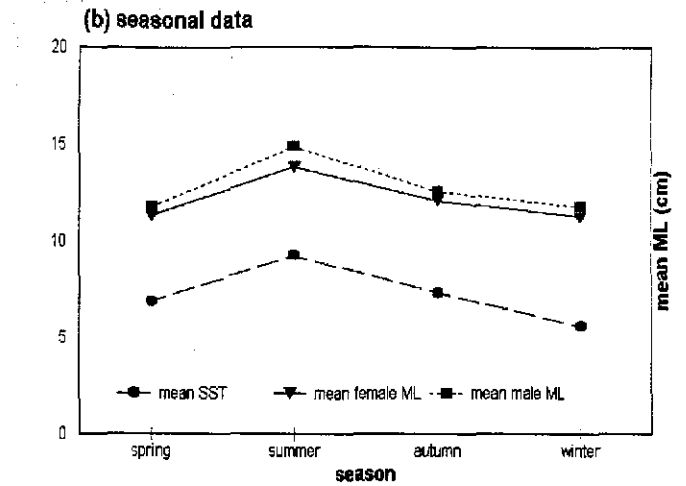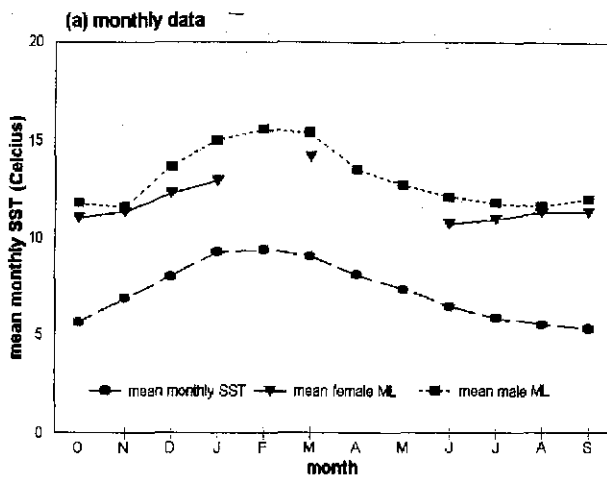
Figure 6. *Loligo gahi.* Relationship between adjusted mean mantle length derived from ANCOVA and mean monthly sea surface temperature (SST) data plotted for data (a) grouped by month of hatch and (b) by season of hatch (see text for exact seasonal groupings).