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Effects on Fish Stocks

SPATIAL VARIABILITY IN THE GROWTH RATE OF BLUE WHITING (*Micromesistius poutassou* (RISSO)) LARVAE AT THE SHELF EDGE WEST OF THE UK

M C Bailey and M R Heath

SOAEFD Marine Laboratory
PO Box 101 Victoria Rd
Aberdeen, AB11 9DB
Scotland, UK

SUMMARY

The distribution of larval blue whiting (*Micromesistius poutassou*) along the shelf edge west of Scotland was mapped during May and June 1994. Age and individual growth histories of larvae were inferred from image analysis of the visible microstructure of the sagittal otoliths. Maximum abundances of larvae were at the shelf break northwest of Ireland and decreased with distance north. There was a consistent relationship between the abundance of larvae and water mass defined by temperature-salinity relationships. Larvae were clearly associated with a tongue of warm-saline water which extended north along the shelf edge. The individual growth rates of larvae within the warm saline water mass were significantly different from those for larvae which were distributed in cooler water in the north of the survey area. The warm water mass contained larvae which were growing faster than those in the surrounding waters. The results indicate that larvae lost from the shelf break zone may suffer higher rates of mortality than those in the warmer waters associated with the Shelf Edge Current, and suggest that the dynamics of the shelf edge water currents may be an important determinant of annual recruitment to the blue whiting stock.

INTRODUCTION

As a result of increasing concern about the sustainability of several of the established fisheries in waters over the continental shelf of western Europe, the need to find new and underexploited fish stocks which can be exploited and managed successfully has become increasingly necessary during the last three decades. Since the 1960's, blue whiting (*Micromesistius poutassou*) found in the vicinity of the shelf break of the north-east Atlantic has been suggested as one alternative to the traditional fisheries situated over the continental shelf. Although comparatively little interest has been expressed in this species by either the international fishing fleets or fisheries biologists, landings of the species caught in the north-east Atlantic have been significant averaging 391.8 x 10^3 t/yr during the period 1981-1995 (Anon, 1996).

If the management of the fishery is to be effective, the determination of the underlying processes affecting early growth and survival of this species is of primary importance in order to aid understanding of the processes affecting recruitment to the parent population. While the cornerstone of fish population management is the assumption of a relationship between recruitment and spawning biomass, fluctuations in the size of fish stocks may occur as a consequence of changes in recruitment. The large variance in recruitment which often confounds any underlying recruitment-stock relationship is often attributed to the effects of environmental variables on the survival of early life stages. Consequently, studies on growth and survival of larvae are important in terms of improving the understanding of natural factors affecting recruitment (Heath, 1992).

Growth in these early life stages can be estimated using otolith microstructure. In the majority of temperate species studied, the deposition of increments within the microstructure of larval otoliths has been shown to be daily (Campana and Neilson, 1985) and is now generally considered ubiquitous (Campana, 1992). Although the exact periodicity of increment formation has not been validated for *M. poutassou*, the estimates of hatch date derived from back calculation of increment counts against julian day number does suggest that a daily frequency of deposition can be assumed under environmental conditions which are normally experienced by this species. In general, the width of each growth increment in an otolith is related to the growth of the fish during the period of deposition. Hence, the width of sequential increments out from the hatch check charts the growth trajectory of the individual up to the time of capture. Physical, chemical or biological fluctuations in the environment experienced by the individual, which had an effect on its growth rate, will be reflected in otolith structure allowing a growth history to be determined (Heath and Bailey, 1995).

METHODS AND MATERIALS

Sampling

The distribution of larval blue whiting along the shelf edge west of Scotland was mapped during May and June 1994 from FRV *GO Sars*. Sampling for fish larvae was carried out with a 1.8 m Methot-Isaacs Kidd Trawl (MIKT) with a mesh size of 1,500 µm (cod-end mesh = 250 µm) towed at four knots. The version of the MIKT used during the survey was fitted with two separate nets with an automatic opening and closing device which was pre-programmed to sample different layers of the water column. One net sampled only the upper 50 m of water, whilst the other sampled the remaining deeper layer to a maximum of 200 m depth. Sampling depth was monitored continually during each deployment using Scanmar depth monitoring equipment. Temperature and salinity were recorded at one second intervals during each deployment by a self-recording conductivity-temperature-depth (CTD) system. This was mounted beneath the plankton sampler in a purpose built frame. At the end of each tow environmental data were downloaded to a PC for later analysis. At every station, a surface water sample was collected from the vessel's non-toxic supply as the sampler entered the water for CTD calibration.

On recovery of the sampler, blue whiting larvae were immediately sorted from the plankton. Larvae were preserved in 80% ethanol buffered to pH 9.2 with Tris base. The remainder of larvae in the sample were sorted into vials and preserved in 80% buffered ethanol. The remainder of the catch including unsorted fish larvae was preserved in 4% buffered

formaldehyde (pH 8.2, borax). Subsequently all fish larvae were sorted from the plankton samples and stored in 80% buffered ethanol.

Counts of blue whiting larvae were normalised to the volume of water filtered for each sample. For each sampling site the concentrations of larvae (m^{-2}) in each depth layer were then averaged after weighting for the layer thickness to give the respective concentration of larvae over the whole depth range covered by the sampler.

Otolith Preparation and Determination of Growth Parameters

The standard length (SL) of individual larvae was measured at x25 magnification using a digitising board connected to a PC. Intact otoliths were removed from each larva using fine dissecting needles viewed through a binocular microscope at x50 magnification. In each case the sagitta and lapillus from each side of the head were isolated and mounted in a thin film of clear nail varnish. The remaining carcase of each larva was dried on an individual pre-weighed aluminium foil pan at 70°C for 48 hours and allowed to cool to ambient room temperature for 24 hours over silica gel before weighing on a microbalance to the nearest 0.001 mg to obtain dry weight (DWT).

Sagittal otoliths extracted from blue whiting larvae were examined under oil immersion at x400 magnification with a Leitz Ortholux II compound microscope attached to an image analysis system (MAGISCAN; Applied Imaging Ltd) giving an on screen magnification of x3,000. The system was programmed to allow the operator to perform a range of morphometric measurements on the otolith. First, the area of the otolith and the radius along the longest axis was recorded. Then the radial distances of each successive increment were measured from the core of the otolith along the longest radius. Finally, the results of the analysis were printed to a file for subsequent analysis in a spreadsheet.

Incremental widths were calculated by subtraction of successive radial distances and related to increment number, counting out from the hatch check mark in the otolith to produce an otolith growth profile. Finally, increment number was related to growth day (ie, the date on which the growth increment occurred), assuming that a hyaline and opaque ring represented a daily growth increment, and that the outer increment represented growth during the day on which the larva was captured.

The otolith growth profiles produced from the incremental widths were smoothed by locally weighted quadratic smoothing using the 15 nearest neighbours (ie, adjacent increment widths), gamma errors and a log link. Mean incremental widths by transect were obtained by pooling the respective smoothed data and dividing by the number of otoliths analysed in each respective transect. Bootstrap pointwise 95% confidence bands were calculated for these means to allow inferences to be made on otolith growth across transects before applying a restricted maximum likelihood (REML) analysis to test for transect effects at the between otolith and between haul levels. The REML analysis was applied at three points during the growth history of the larvae, these being at 1, 10 and 20 days post hatch.

RESULTS

Distribution of Larvae

The distribution of blue whiting larvae present in the top 200 m of the water column throughout the survey area is shown in Figure 1. Highest concentrations of larvae were found in the south along transect A with a peak density of 130 larvae /m^2 at station 7 (56°30'N, 10°45'W). With increasing distance north the concentrations of larvae fell to a minimum of 0.3 larvae/m^2 at station 30 (60°10'N, 03°50'W) whereafter no further blue whiting larvae were encountered.

Temperature and Salinity

Although larvae were sampled down to 200 m, spatial differences in water temperature were most marked in the 0-50 m layer. As it is reasonable to assume that all the larvae used in the analysis will have spent a large proportion of the day feeding in the top 50 m where a food supply (eg copepod nauplii) is likely to be most abundant, the averaged 0-50 m temperature and salinity data were used and presented in Figures 2a and 2b respectively. The hydrographic data showed the clear influx of warm high salinity water flowing north along the shelf edge with colder lower salinity oceanic water further to the north, east of Faroe. Typically, sea temperatures in the vicinity of transects A and B were in excess of 9°C with salinity higher than 35.25‰. Along transect D where the most northerly blue whiting larvae were found at the lowest density, both temperature and salinity had fallen by 0.5-1.0°C and 0.1‰ respectively. Areas of much colder low salinity water were found in the inshore areas of the northern North Sea and the North Sea outflow located over the Norwegian Deeps.

The relationship between the temperature and salinity of the survey area and the distribution of blue whiting larvae is shown in Figure 3. This is a conventional temperature-salinity plot with the concentration of larvae expressed as n/m^2 in the 0-200 m layer superimposed. It is apparent that the distribution of larvae was clearly associated with the warmer high salinity water of the shelf edge current (SEC). The relationships shown in Figure 3 also suggest the presence of upto three additional water masses in the survey area; the cooler high salinity oceanic water of the north-east Atlantic to the bottom right; the North Sea outflow water to the centre; and the low salinity waters of the inshore areas of the North Sea to the left of the figure.

Length - Weight Relationships

The results of the length and dry weight analysis showed a linear relationship (Fig. 4) when the variables were transformed to their natural logarithms ($r = 0.836$, $n = 421$) producing the equation:

$$\ln DWT = -5.773 + \ln SL$$

ANCOVA of the untransformed data with DWT as the dependent variable and SL as the covariate revealed significant differences in weight at length between transects ($p<0.001$) and also showed significant latitudinal differences in SL ($p<0.001$) across transects (Table 1). Median SL and DWT were greatest from larvae taken on Transect A and showed a general decrease with distance north. Larvae from Transect A were significantly longer (median SL = 8.7 ± 1 SD = 1.8 mm) and heavier (median DWT = 0.49 ± 1 SD = 0.47 mg)

than larvae from Transects B (7.2 ± 1.41 mm, 0.47 ± 0.43 mg) and C (6.4 ± 0.9 mm, 0.34 ± 0.18 mg) respectively, and this trend is supported in general by the results of the Tukey post-hoc pairwise comparisons presented in Table 2.

In Table 2 it can be seen that significant differences in weight at length were present between larvae from transect A and larvae from transects B and C. However, there was no significant difference between larvae from transects A and D and transects B, C and D and the similarity in weight at length between larvae from transects A and D should be noted. The influence of the colder Atlantic oceanic water mixing with the warm high salinity water of the Shelf Edge current and therefore reducing the water temperature was expected to be detrimental to the growth of larvae in the north of the study area. However, the total number of blue whiting larvae caught on transect D was low (n = 6) and from a single station, so although no significant difference was found between the weight at length of larvae from transect A and transect D, due to the low number of larvae obtained on transect D it was not possible to determine whether this result was representative.

Otolith Analysis

Otolith radius - fish weight relationship

Figure 5 shows that the relationship between DWT and the square of the otolith radius (RADSQ) used in the incremental analysis was also linear (r = 0.865, n = 385) producing the equation:

$$RADSQ = 680.63 + DWT$$

ANCOVA with RADSQ as the dependent variable and DWT as the covariate showed no significant differences between transects ($p>0.5$) though there were significant latitudinal differences in DWT between transects ($p<0.001$). The results of this analysis are presented in Table 3.

The constant relationship of RADSQ to DWT across transects together with the significant spatial differences found in DWT at SL suggested that otolith growth was more representative of skeletal growth than somatic growth.

If otolith radius was more representative of skeletal growth, and hence SL across transects, then the significantly greater weight at length of larvae from Transect A, and to some extent Transect D, indicated that these larvae were in better condition than larvae from the other transects.

Hatch Date Distribution

By assuming a daily periodicity of increment deposition within the otoliths, in addition to obtaining age at capture it was also possible to back-calculate the date of hatching of the larvae used in the analysis. The hatch date distributions of larvae from each transect are shown in Figure 6. In addition to the overall linear relationships shown in Figures 4 and 5, the narrow range in median hatch day number (julian days 111-116) across all four transects also supported the assumption that all the larvae used in the analysis came from the same spawning event which may have been distributed across a wide latitudinal range.

Analysis of Growth from Incremental Widths

Mean smoothed increment widths by transect are shown in Figure 7 together with the respective Bootstrap 95% confidence bands. Overall growth rate varied systematically with age with a general rapid increase in increment width during the second and third weeks of growth. At day 1 there was no significant transect effect (Wald statistic = 1.2, df = 3, p = 0.75) which was still evident at day 10 (Wald statistic = 2.6, df = 3, p = 0.46). However, by day 20, having adjusted for the widths at days 1 and 10, a significant transect effect was found (Wald statistic = 6.2, df = 3, p = 0.03). This could be summarised by a linear trend in mean transect temperature of 0.88 μm/°C. These statistics support the observations presented in Figure 8 where during the first 10 days of growth there was no discernable difference in incremental width between transects however, by day 15 it is apparent that larvae form Transect D (station 30) had narrower increments than larvae of the same age from Transects A, B and C. By day 20 a clear latitudinal trend in the growth trajectories had emerged where the larvae in the north of the study area were growing at a significantly slower rate than larvae further to the south. Although the low number of larvae from Transect D may be unrepresentative from a statistical view point, the fact that they had markedly narrower increments in their otoliths from approximately day 10 which became significant by day 20 did suggest that they were growing at a significantly slower rate than larvae further to the south in the study area and were therefore at a disadvantage to these more southerly distributed larvae in the warmer waters of the SEC.

DISCUSSION

The origins of growth rate variability in larval fish are of key importance to understanding recruitment variations in fish stocks. This is because mortality may be closely related to growth rate. Reductions in growth rate increase the stage duration and expose individuals to predation pressure for longer periods, thereby reducing survival to any further specific size or developmental stage.

The most likely sources of growth rate variability in the field seem to be temperature and food abundance. However, other factors cannot be ruled out, such as food quality or parental effects. Another important unknown factor is the role of density dependance, and whether this plays any role in determining individual growth rates. An important priority for field studies is an assessment of the dominant factors affecting different species in differing circumstances.

In this study, we demonstrate the existence of spatial variations in daily growth rates of blue whiting larvae. However, as with all such studies it is difficult to ascertain exactly what factors are responsible. Latitude provides the simplest correlation, although there is no reason to suppose that latitude *per se* is responsible. Almost certainly, latitude is an analogue for the actual factors determining growth rate. In this particular circumstance, temperature is closely related to latitude, and may well be the major factor. Nevertheless, across-shelf variations in temperature were not related to growth rate although the contrast in temperature across the shelf was small compared to that along the shelf.

The conclusion that temperature was probably a major determinant of blue whiting larval growth rates at the shelf edge in no sense implies that we do not believe food and many other factors are involved, and it is possible that these other factors may also be aliased with temperature. From their otolith microstructure, larvae from Transect D appeared to

be growing at a slower rate than larvae from the other transects although there is evidence to suggest that these larvae were in better condition at length that the larvae from Transects B and C. The low number of larvae obtained from Transect D does not allow clear conclusions to be drawn, but the lower density of larvae in the north of the survey area could be partly responsible. Investigating the role of prey abundance is far from simple and would involve analysis of the stomach contents of larvae and a comparison of the incidence in the water column of the species and sizes of prey consumed. Analysis of zooplankton samples collected during the cruise has been carried out, but stomach contents have not yet been examined.

The overall distribution of blue whiting larvae was in agreement with long term historical records and more recent surveys; eg McFadzen and Cook (1996). In the light of such data the high densities of larvae seen to the west of Scotland in 1994 suggest that this is an area of established spawning activity and that spawning takes place over an extended latitudinal area. This is supported by the distribution of back-calculated hatch date which did not show any marked latitudinal cline with age. This suggests that larvae hatched along the shelf edge rather than in an area of prolific spawning intensity further to the south; however, the rate of passive transport of eggs and larvae may have been variable with depth causing recently hatched larvae to be transported north at a faster rate than older larvae at the surface producing the distribution of hatch dates seen in this study. Although the general directional movement of the SEC in the survey area is known to flow north as a homogenous body of water extending from the surface to the seabed, there is a little evidence to suggest variability of current speed with depth. Mean current speed has been shown to vary from 6 to 30 cm/s with increasing latitude from Malin (56°N) to west of Shetland (60°N) over the 1,000 m contour (Huthnance, 1986) while Turrell *et al.* (1992) demonstrated that for the area northwest of the Hebrides, where the salinity core of the current was situated above the 300 m contour, along slope current speeds increased further offshore. They found that on average, current speeds increased from 10 cm/s to 20 cm/s as bottom depth increased from 200 m to 500 m. Furthermore, wind-shear has been suggested a contributing factor to the distribution of particles in the surface waters of the SEC (Bartsch and Coombs, 1996). Walsh *et al.* (1996) clearly indicate a southerly mean average flow in May over the 1976-1994 period for the 0-20 m depth layer. Clearly such studies have implications for larval retention in the surface waters over the shelf break west of Scotland. Coombs *et al.* (1981) showed that eggs of blue whiting over the shelf edge can be distributed over a wide range in depth (200-500 m) although they found that there was a marked negative relationship between depth and length class. Small larvae (<2.5 mm) were found in the water column mainly between 300-500 m while larger larvae (5.1-7.5 mm) were caught almost exclusively in the 0-40 m layer. It may be possible therefore, that any variability in the rate of transport occurring at depth (200-500 m) caused the small, young larvae to be transported north at a different rate than older larvae which had hatched earlier and completed their vertical migration to the surface. If this rate of transport was faster, any latitudinal cline in age which might be expected would have been obscured. Reduced water temperature has been shown to delay hatching considerably in this species (Coombes and Hiby, 1979; Seaton and Bailey, 1971) and it is not unreasonable to assume that eggs spawned and retained at depth may have been subjected to both variability in current speed and cooler temperatures. These factors could have contributed markedly to the observed distribution of back calculated hatch date and growth rate.

Accepting these cautions, our results add further weight to existing published studies which show that temperature can account for the major part of growth rate variations in the field, for example, cod and haddock larvae in the northwest Atlantic (Campana and

Hurley, 1989), striped bass in Chesapeake Bay (Rutherford and Houde, 1995), pollock in Alaska (Haldorson *et al.*, 1989), plaice in the North Sea (Hovenkamp and Witte, 1991). On shorter time scales and smaller space scales where temperature variations are small, a range of other factors including prey density (Govoni *et al.*, 1985) and turbulence (Gallego *et al.*, in press) may assume increased importance.

ACKNOWLEDGEMENTS

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TABLE 1

ANCOVA of dry weight with standard length as the covariate by transect

Source	Sum of squares	df	Mean square	F ratio	p
Transect	7.576	3	2.525	58.001	<0.001
SL	50.703	1	50.703	1164.550	<0.001
Error	18.112	416	0.044		

TABLE 2

Tukey post hoc pairwise comparison ($p > 0.05$) showing non-significant differences in dry weight at length for blue whiting larvae sampled from each of the four transects

A	D	B	C

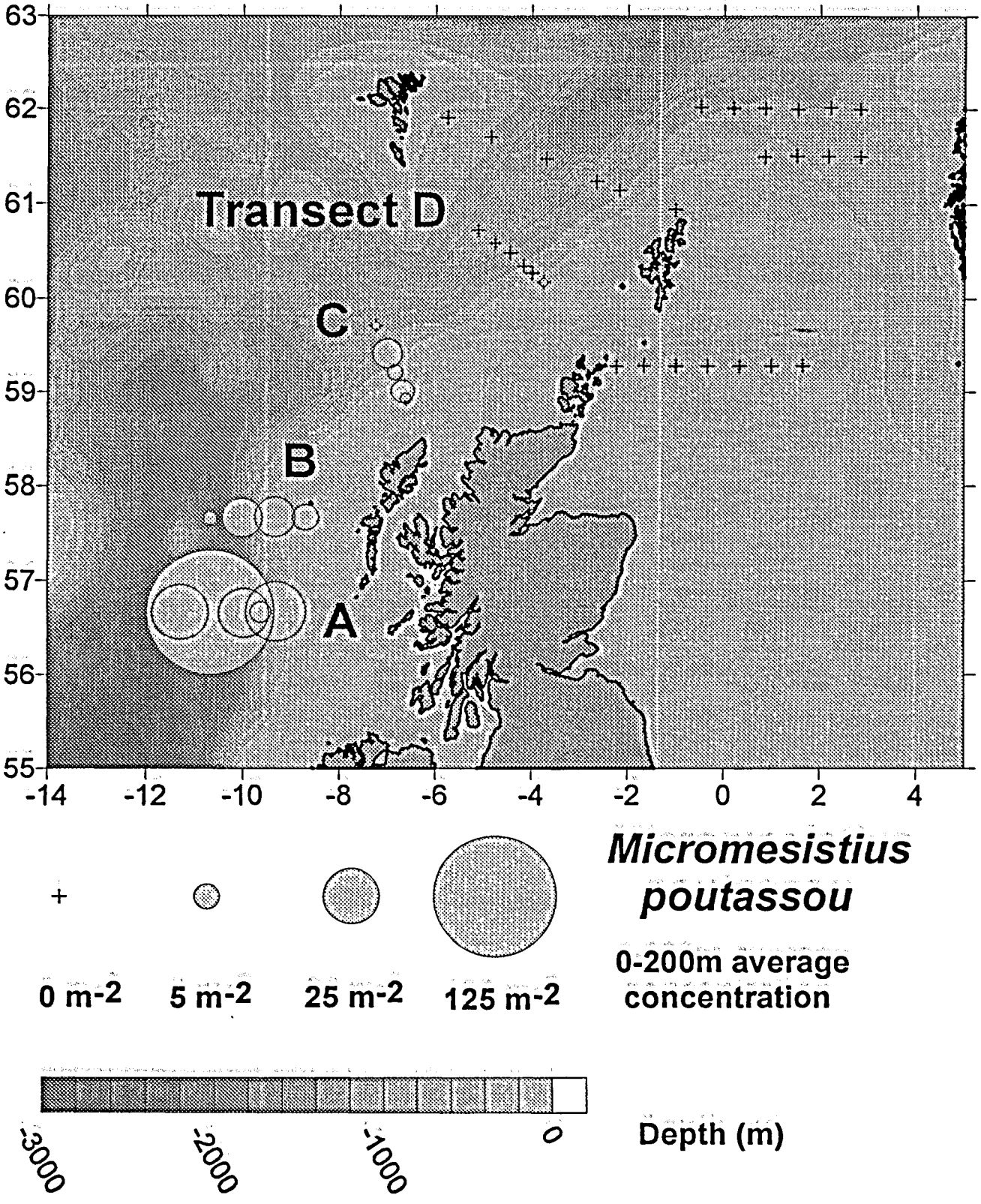
TABLE 3

ANCOVA of the square of otolith radius with dry weight as the covariate by transect

Source	Sum of squares	df	Mean square	F ratio	p
Transect	4.696 E+6	3	1.565 E+6	0.768	0.512
DWT	2.178 E+9	1	2.178 E+9	1069.253	<0.001
Error	7.741 E+8	380	20.37 E+6		

LIST OF FIGURES

Fig.1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2
4
Transect D
C
B
A
Micromesistius poutassou
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Depth (m)

Fig.2a

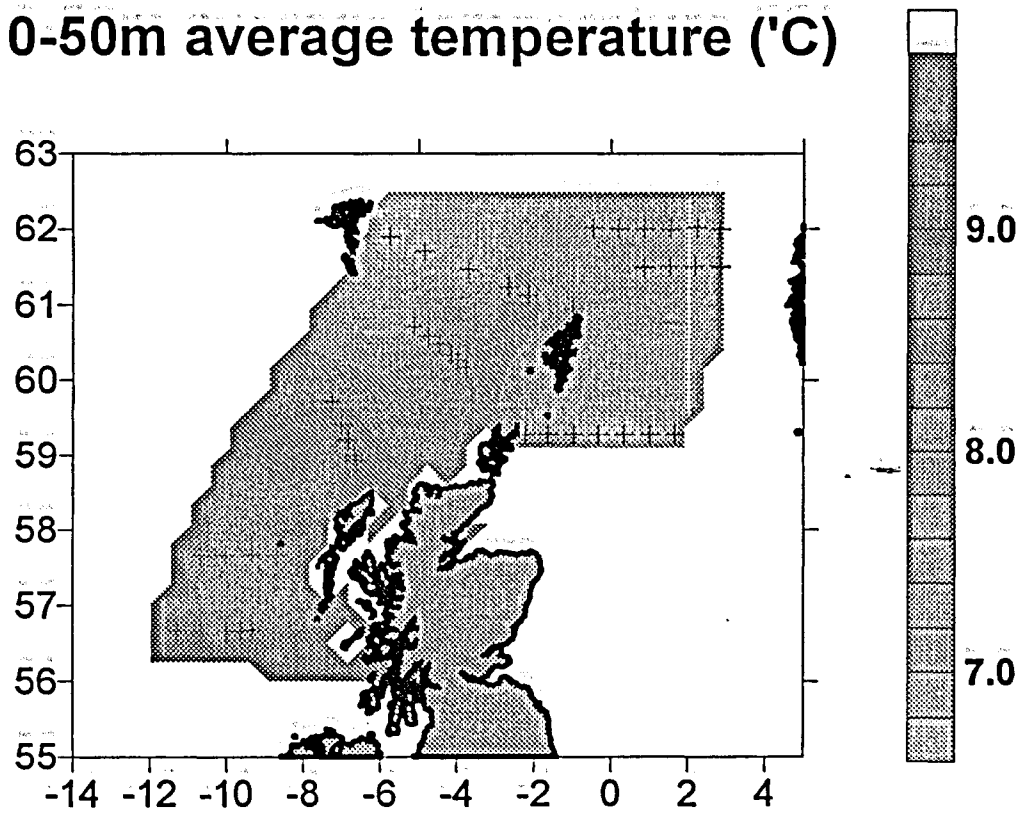
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Fig.2b

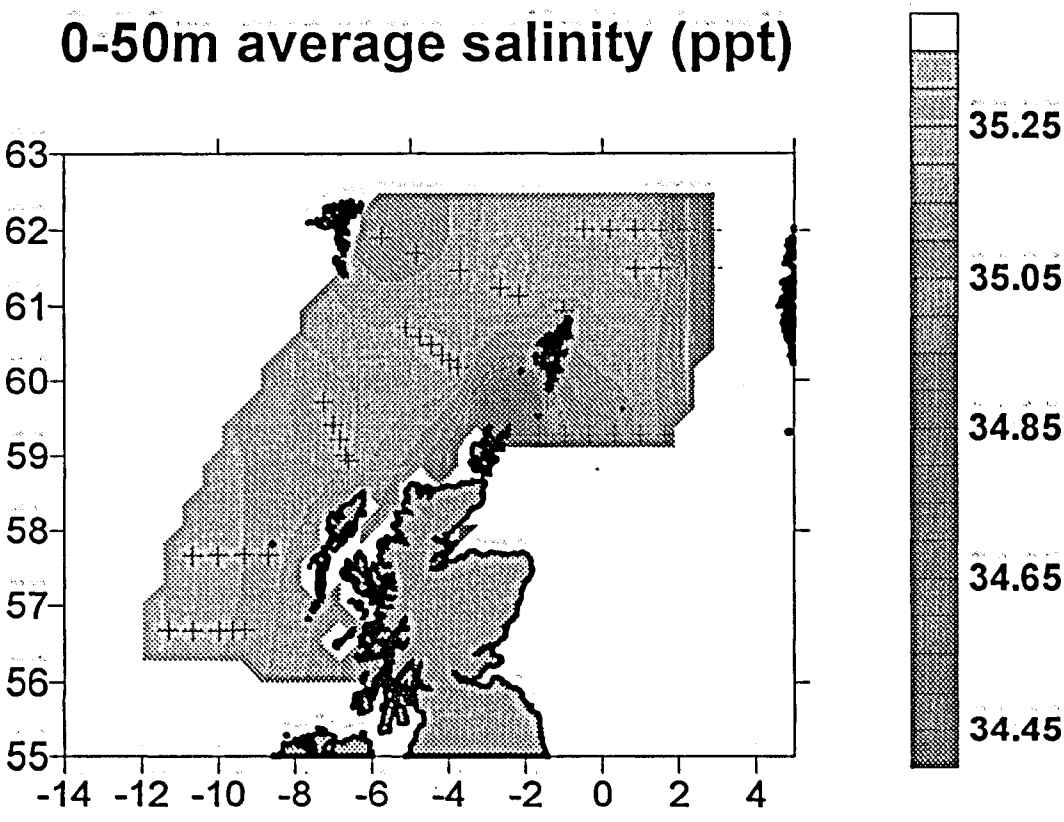
0-50m average salinity (ppt)
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Fig.3

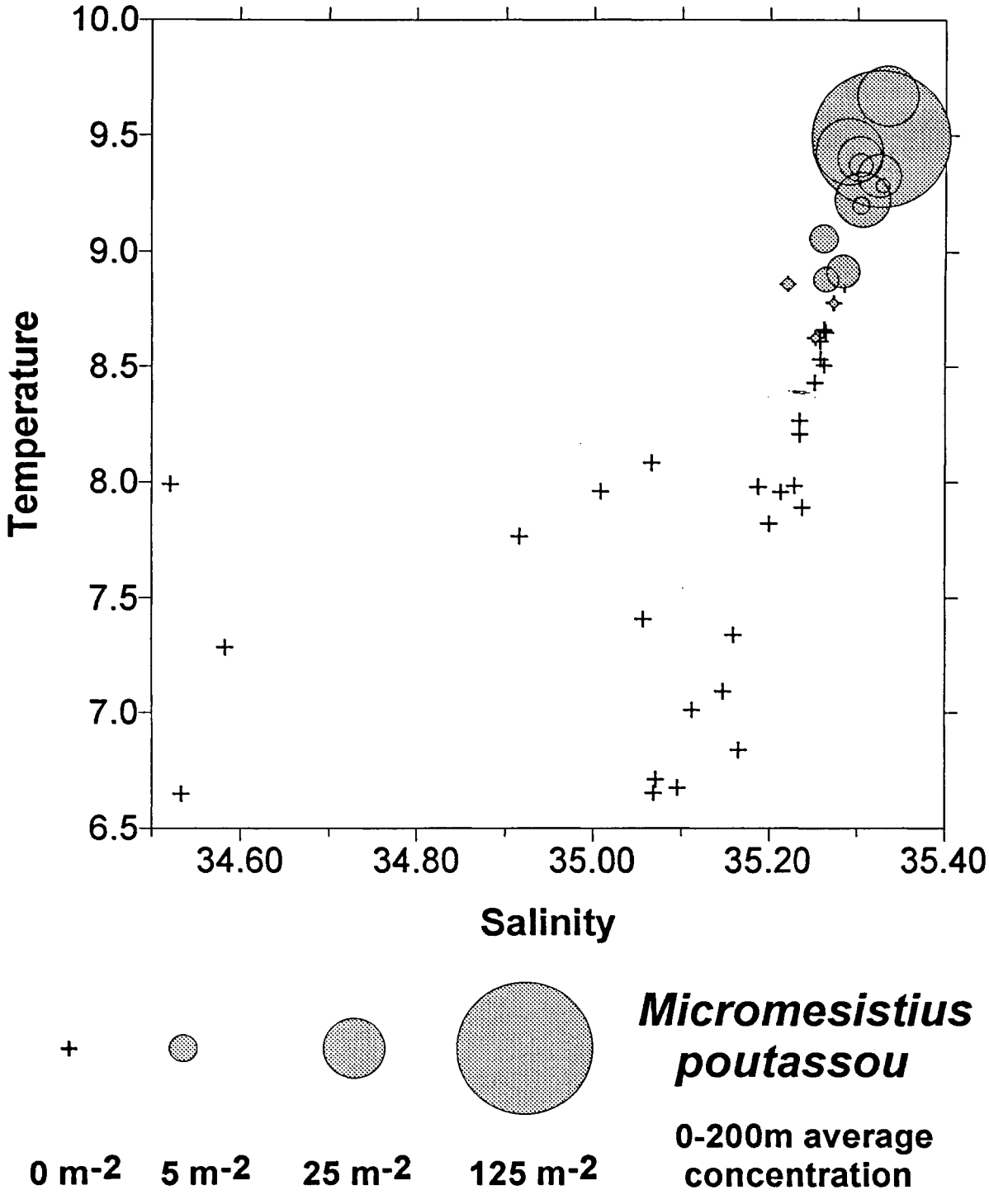
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Fig.4

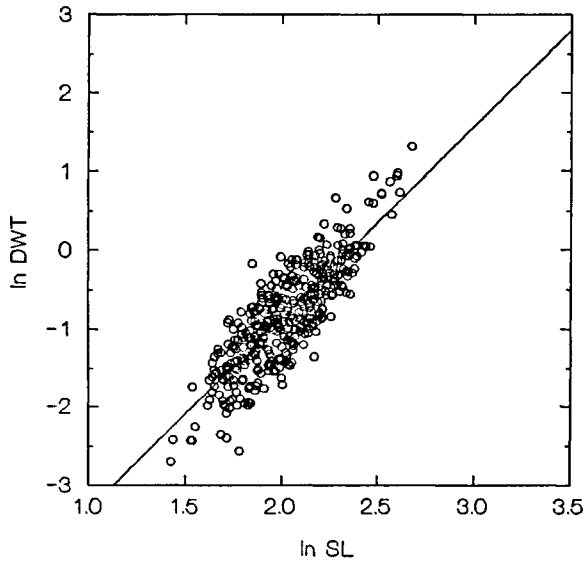
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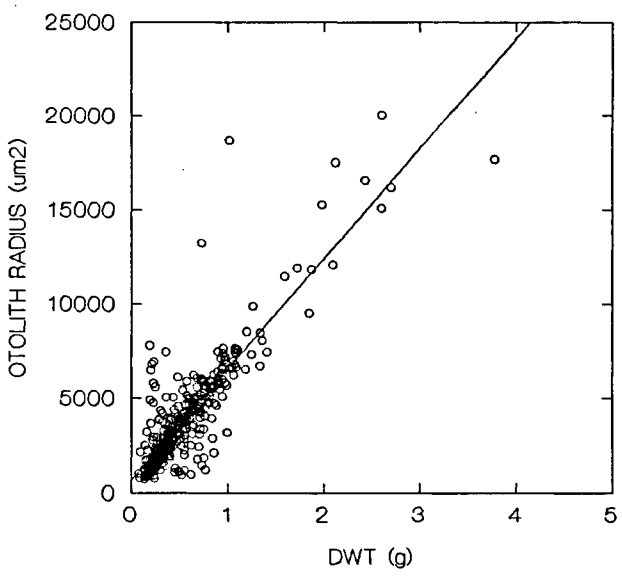
Fig.5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OTOLITH RADIUS (um2)
DWT (g)

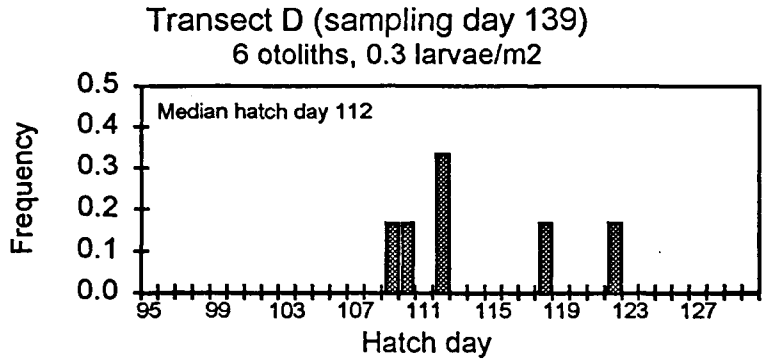
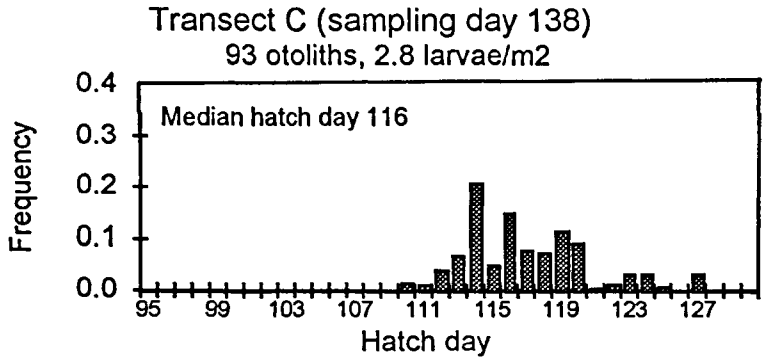
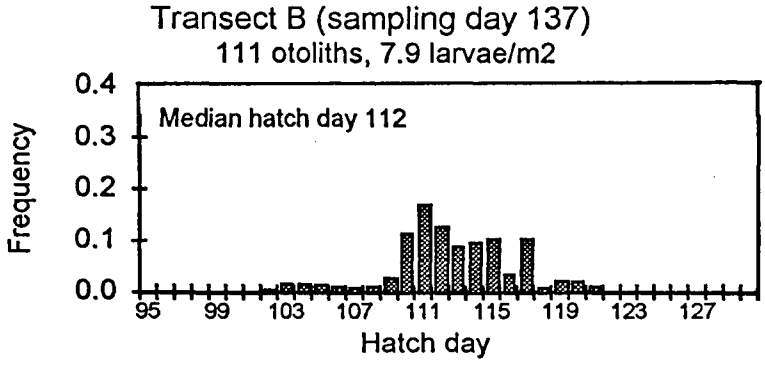

Transect D (sampling day 139)
6 otoliths, 0.3 larvae/m2
Median hatch day 112
Frequency
0.5
0.4
0.3
0.2
0.1
0.0
95 99 103 107 111 115 119 123 127
Hatch day

Fig.6


Transect C (sampling day 138)
93 otoliths, 2.8 larvae/m2
Median hatch day 116
Frequency
0.4
0.3
0.2
0.1
0.0
95 99 103 107 111 115 119 123 127
Hatch day


Transect B (sampling day 137)
111 otoliths, 7.9 larvae/m2
Median hatch day 112
Frequency
0.4
0.3
0.2
0.1
0.0
95 99 103 107 111 115 119 123 127
Hatch day

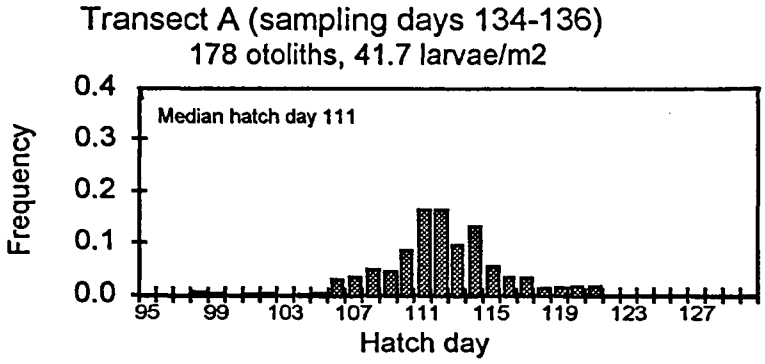
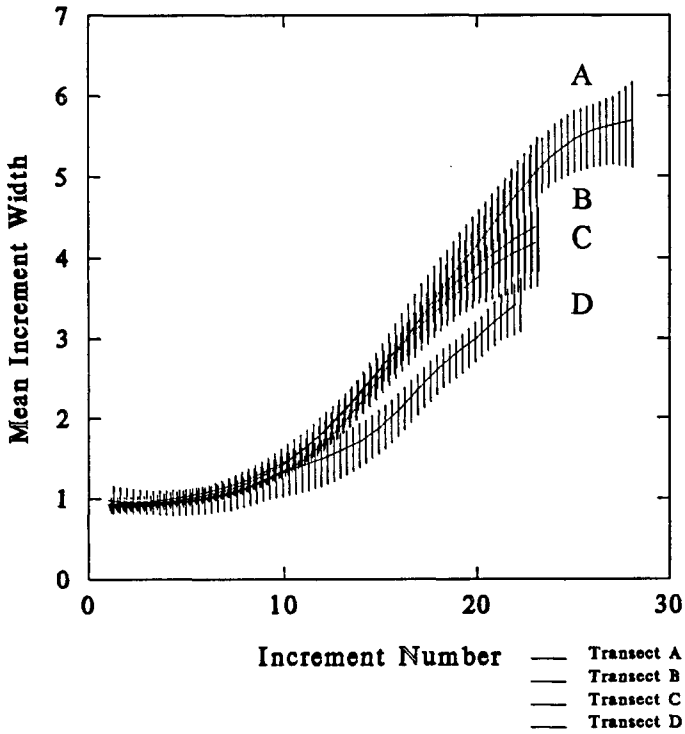

Transect A (sampling days 134-136)
178 otoliths, 41.7 larvae/m2
Median hatch day 111
Frequency
0.4
0.3
0.2
0.1
0.0
95 99 103 107 111 115 119 123 127
Hatch day

Fig.7


Mean Increment Width
0
1
2
3
4
5
6
7
0
10
20
30
Increment Number
A
B
C
D
Transect A
Transect B
Transect C
Transect D