

THE IMPACT OF ENVIRONMENTAL GRADIENTS ON THE EARLY LIFE INSHORE MIGRATION OF THE SHORT-FINNED SQUID *ILLEX ILLECEBROSUS*

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Recruitment of the short-finned squid *Illex illecebrosus* to adult feeding grounds on the shelf off eastern Canada constitutes an important transition from warm food-limited Gulf Stream waters to cold and productive slope and coastal waters. The impact of such gradients was addressed by analysing the gladius growth of 1585 juvenile squid collected across the Gulf Stream and shelf/slope fronts during research cruises conducted between 1979 and 1989. Temperature- and size-specific growth potential, as estimated by a bioenergetics model, were compared to measured gladius growth rates and revealed that young *Illex* were energetically expensive and food-limited in Gulf Stream waters (their hatching environment). Growth condition improved inshore, where metabolic costs decreased and more food became available. Similar patterns were observed when size-specific growth rates of squid caught across the temperature and food gradients were directly compared. In addition, transport processes in the Gulf Stream and slope water played an important role in providing access and retention in favourable areas. Juvenile onshore migration seems to be driven by elevated food requirements and involves physiological adaptations to compensate for decreasing temperatures. The individual "success" in terms of growth and survival may depend, however, on access to concentrated patches of food which, in turn, will be determined by timing and the transport dynamics of the main water masses.

The short-finned squid *Illex illecebrosus* has sustained a valuable but highly unpredictable fishery in the North-West Atlantic (Black *et al.* 1987, O'Dor and Dawe 1998). Like other ommastrephid squid, *I. illecebrosus* is short-lived, semelparous and annual; recruitment is dependent on the reproductive success of each generation and determines the population abundance each year (Amaratunga 1983, 1987). Losses during the planktonic early life may affect the processes of recruitment. Their causes, however, have seldom been addressed empirically and are mostly hypothesized from patterns established for other marine populations with complex life cycles (Vecchione 1991, Bakun and Csirke 1998).

Understanding of the early life history of *Illex illecebrosus* derives from observations of paralarvae hatched in captivity (O'Dor *et al.* 1986), studies of post-embryonic development (Nesis 1979, Roper and Lu 1979, Vecchione 1979) and considerable data on the seasonal, spatial and vertical distribution of early life stages in the NW Atlantic (Fedulov and Froerman 1980, Amaratunga 1981, Froerman *et al.* 1981, Dawe *et al.* 1982, Dawe and Beck 1985a, b; Hatanaka *et al.* 1985, Rowell *et al.* 1985). Spawning occurs throughout the year over the Blake Plateau, south of Cape Hatteras (34°N). Eggs enclosed in neutrally buoyant gel masses are carried north by the Gulf Stream, where embryonic development and hatching takes place. The

early life is spent along the meandering northern boundary of the Gulf Stream and the slope waters, and it ends when the offspring reach the adult habitat on the continental shelf. During this transition, offspring are subject to important temperature and food availability gradients, as determined by their encountering distinct water masses. The squid being provided with limited yolk supply and an energetically expensive life-style (O'Dor *et al.* 1986), such gradients may impose serious limitations on the attainment of required growth rates and survival during the early life. The aim of this study is to evaluate the impact of temperature and food gradients on the growth of the short-finned squid during its early life, inshore migration off eastern Canada in spring.

MATERIAL AND METHODS

The Gulf Stream/ slope water front

The environment experienced by the early stages of *Illex illecebrosus* is characterized by dynamic interaction of distinct water masses in the NW Atlantic. The physical properties and the circulation patterns of such waters have been described by McLellan (1957), Gatien (1976), Horne (1978), Csanady and Hamilton

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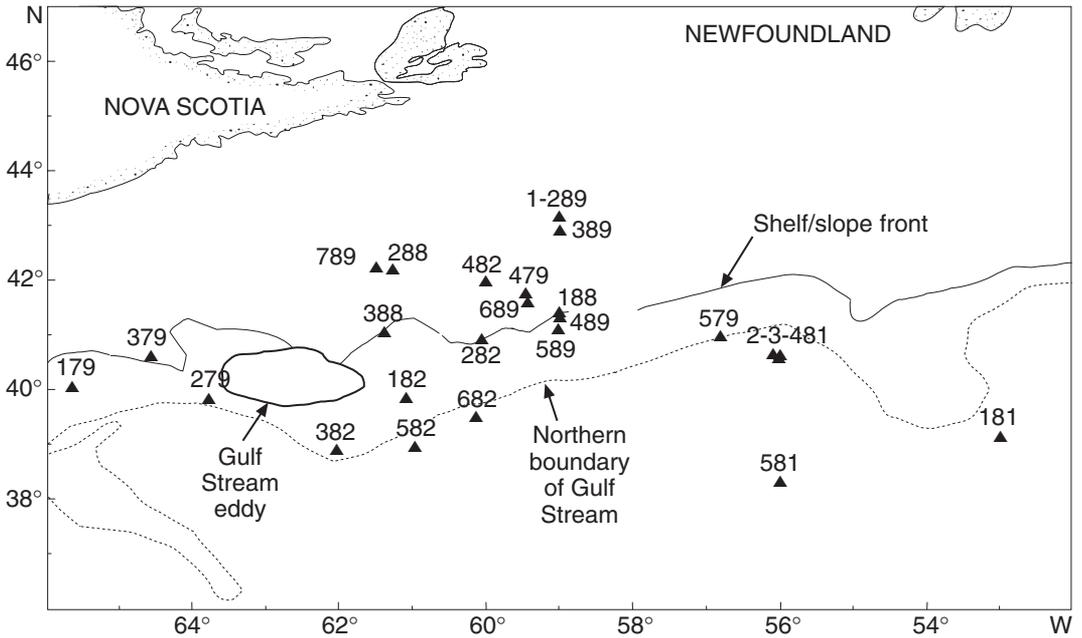


Fig. 1: Study area and positions where juvenile *Illex illecebrosus* were sampled. The physical environment around the fishing stations can be described partially by daily positions of the northern boundary of the Gulf Stream, the shelf/slope front and the Gulf Stream eddy activity derived from NOAA satellite thermal imagery (Drinkwater *et al.* 1994). Numbers represent the sample and (last two digits) year of sampling. Latitudes and longitudes are decimal-transformed

(1988) and others. Warm waters of the NE-flowing Gulf Stream and Sargasso Sea (temperatures and salinities $>15^{\circ}\text{C}$ and $>35 \times 10^{-3}$ respectively) occupy the offshore area south of 40°N . Influenced by continental freshwater run-off and the south-flowing Labrador Current, coastal waters overlie the continental shelf, exhibiting temperatures and salinities below 10°C and 35×10^{-3} respectively. Warm slope waters, of intermediate temperatures and salinities, flow north-east and occupy superficial layers between the Gulf Stream and coastal waters. Beneath the warm slope water, cold Labrador Slope Waters overlie the slope, and the North Atlantic Central Water mass extends seawards towards the Sargasso Sea.

The area of contact between the Gulf Stream and the warm slope water is characterized by a sharp thermal gradient (the "wall" of the Gulf Stream) that slopes down seawards from the surface to depths of 800 – 1 000 m. Shorewards, the shelf/slope front marks the encounter of warmer and more saline slope waters with colder and less saline coastal waters. The latter water mass extends over the slope waters at the surface and the front slopes down shorewards, meeting the sea floor

near the shelf break. Surface positions of the shelf/slope front and the northern boundary of the Gulf Stream fluctuate around 38 and 41°N (Fig. 1) and reach maximum onshore positions annually during late summer and autumn (Drinkwater *et al.* 1994). Both fronts are also characterized, at the surface, by irregularities related to the meandering behaviour of the Gulf Stream. Particularly important features, associated with mechanisms of exchange between water masses, include eddies attached to the Gulf Stream and rings spun off them. Seasonal levels of primary and secondary production vary spatially and are associated with physical and biological characteristics of each water mass and physical processes of the fronts (Mann and Lazier 1991). In general, coastal and slope waters are more productive and conditions are particularly enhanced at the fronts (Fournier 1978, Raymont 1980, 1983).

Origin of samples and environmental data

This study was based on 26 samples of juvenile short-finned squid *Illex illecebrosus* collected during

Table I: Summary of information from the samples used for evaluation of environmental gradients on early growth of short-finned squid *Illex illecebrosus*

Vessel	Month	Area	Number of squid	Mantle length range (mm)
R.V. <i>Belogorsky</i>	March 1979*	Nova Scotia	149	11.8 – 65.4
R.V. <i>Gadus atlantica</i>	February 1981*	Newfoundland	303	11.1 – 30.1
R.V. <i>Lady Hamilton</i>	February 1982*	Nova Scotia	336	10.6 – 43.8
R.V. <i>Needler</i>	January 1985	Florida	121	7.8 – 57.4
R.V. <i>Needler</i>	February 1988*	Nova Scotia	81	11.0 – 60.2
R.V. <i>Needler</i>	April 1989*	Nova Scotia	297	18.7 – 92.3
R.V. <i>Needler</i>	June 1989	Nova Scotia	60	18.8 – 67.9
R.V. <i>Needler</i>	August 1989	Nova Scotia	59	30.6 – 46.5
F.V. <i>Rio Salado</i>	June 1991	Nova Scotia	58	119.0 – 192.0
F.V. <i>Rio Damuji</i>	June 1991	Nova Scotia	61	118.0 – 188.0
R.V. <i>Petrel</i>	June 1991	Nova Scotia	60	143.0 – 201.0
Total			1 585	7.8 – 201.0

* Samples used for recent growth analysis

six research cruises conducted in the late winter and spring of 1979, 1981, 1982, 1988 and 1989 (Table I). The area surveyed was bounded by latitudes 44 and 37°N and by longitudes 66 and 52°W, extending from the Scotian Shelf along the shelf break into the northern edge of the Gulf Stream (Fig. 1).

In 1979, 1981 and 1982, the surveys were directed at *I. illecebrosus*, and the main objective was to investigate the geographical and diel distribution of paralarvae and juveniles in relation to the hydrographic structure in the vicinity of the Gulf Stream and the shelf/slope fronts. Squid were caught by means of an Engels Midwater Trawl (1979–1981) and a 510 Pelagic Trawl (1982) in tows distributed along north-south transects at 50, 100, 200, 300, 500 and 1 000 m depth strata. Details of sampling procedures and data collection are given by Amaratunga *et al.* (1980), Dawe *et al.* (1981), Amaratunga and Budden (1982) and Dawe and Beck (1985a). The 1988 and 1989 cruises were part of a series of surveys with the purpose of investigating the distribution of mesopelagic fauna in slope and coastal waters. Stations were distributed along five transects and fishing was conducted using an International Young Gadoid Pelagic Trawl (IYGPT) in a stepped oblique pattern at 200, 100 and 50 m depths (D. Themelis, Mt St Vincent University, Halifax, Canada, pers. comm.).

Squid samples were fixed in formalin and preserved in ethanol (approximate concentrations 10 and 70% respectively), and were part of historic collections maintained at the Department of Fisheries and Oceans (St John's, Newfoundland, and Halifax, Nova Scotia) and at the Atlantic Reference Center (Huntsman Marine Biological Station, New Brunswick). When samples in a single cruise were numerous, they were selected according to their position across the Gulf Stream boundary and shelf/slope fronts. Large samples were

subsampled for growth analysis.

The physical environment around the fishing stations, including the position of the northern boundary of the Gulf Stream, the shelf/slope front and the Gulf Stream eddy activity, was described from (a) hydrological data collected along the transects and (b) climatic data for the NW Atlantic derived from NOAA satellite thermal imagery (Drinkwater *et al.* 1994). The shortest distance measured from the fishing stations to the Scotian Shelf (DSH – defined by the 200 m isobath) and the daily positions of the Gulf Stream (DGS) and the shelf/slope front (DSS), were used as indices of juvenile “penetration” into the adult coastal habitat. The distances were measured on a navigation chart and were given positive/negative signals according to their onshore/offshore position in relation to the oceanographic fronts (Fig. 1). The shortest distance between the fishing stations and the daily position of the nearest eddy (DNE) was used to represent the association of the samples with Gulf Stream eddy activity. When positions of oceanographic fronts and eddies were not available for specific days, the distances were averaged from the data of approximately one week available within the vicinity.

Gladius analyses and numerical representation of growth

Juvenile growth was estimated from analysis of the gladius accretive growth according to the methodology described in Perez *et al.* (1996). The gladius was dissected out from preserved juveniles and fresh-frozen subadults and prepared for increment interpretation. Gladii were measured for total length *GL* and their growth increments (*GInc*) were observed under a dissecting microscope and measured in micrometres

Table II: Comparison of juvenile squid *Illex illecebrosus* recent growth index (RGI) in five surveys off the Scotian Shelf. The ANCOVA tested for differences of mean RGI ("Between Subjects") and of mean recent growth profiles ("Within Subjects"), i.e. RGI was considered as repeated measures within each squid gladius among samples examined in each survey. SAMPLE was the grouping factor, DAYS the time period during which RGI was measured repeatedly (15 growth increments or "days") and GL_i was the covariate that represented the gladius length at the beginning of the measured growth period. Degrees of freedom (df) and mean squares (MS) are also indicated

Source	1979		1981		1982		1988		1989				
	df	MS	df	MS	p	MS	df	MS	p	MS			
Between Subjects	1	0.009	1	0.021	0.449	1	0.089	1	0.302	0.091	1	0.086	0.101
SAMPLE × GL_i	14	0.001	14	0.002	0.338	14	0.001	14	0.002	0.909	14	0.002	0.381
Within Subjects													
DAYS × SAMPLE × GL_i	4	0.059	4	3.060	<0.001*	5	0.164	2	0.694	0.001*	6	0.831	<0.001*
	1	0.340	1	0.225	0.003*	1	1.461	1	0.975	0.001*	1	21.200	<0.001*
Within Subjects													
DAYS	14	0.001	14	0.001	0.837	14	0.001	14	0.002	0.897	14	0.007	<0.001*
DAYS × SAMPLE	56	0.001	56	0.002	0.887	70	0.002	28	0.003	0.906	84	0.001	0.947
DAYS × GL_i	14	0.001	14	0.001	0.866	14	<0.001	14	0.003	0.723	14	0.024	<0.001*

* Significant ($p < 0.05$)

Homogeneity of slopes

ANCOVA

using an Image Analysis System (Bioscan®-Optimas). On each gladius, a series of $GInc$ was reconstructed from the gladius anterior border towards the posterior end until the marks became faint. $GInc$ series were smoothed using a statistical low-pass filter, where each filtered i^{th} increment resulted from the sum of three consecutive weighted values: $0.25GInc_{i-1} + 0.5GInc_i + 0.25GInc_{i+1}$. Filtered $GInc$ represented the gladius absolute growth rate during one day (see Perez *et al.* 1996 for analysis of accuracy).

The general effect of environmental transitions on growth was addressed by comparing size- and temperature-specific Daily Growth Potentials (DGP) with growth rates measured on the gladius structure. This analysis was initially conducted by estimating DGP s from the energetic budget equation (O'Dor and Wells 1987):

$$DGP = FR - MR \quad (1)$$

where DGP results from the difference between *ad libitum* feeding rates FR and metabolic rates MR , both expressed in Kcal·day⁻¹ and calculated empirically as a function of mass W and temperature t at a given i^{th} day:

$$MR_i = 0.0043(W_i^{0.96})1.187^t \quad (2)$$

$$FR_i = 0.058(W_i^{0.79})1.082^t \quad (3)$$

Assuming 1 Kcal·g⁻¹, DGP estimates the potential absolute growth in grammes per day (O'Dor and Wells 1987). Daily back-calculated GL were transformed into W_i by the relationship $W = 0.000035GL^{2.799}$ (Perez *et al.* 1996) and used to calculate size-specific DGP at different temperatures. Size- and temperature-specific "potential" and "observed" growth rates were compared after transforming $GInc$ and DGP respectively into Instantaneous Growth Rate G by the equation

$$G = 2.799(\ln GL_{i+1} - \ln GL_i) \quad (4)$$

for $GInc$, and the approximation

$$G = DGP_i/W_i \quad (5)$$

for DGP when the time interval i is 1 (Ricker 1979). The difference between potential and observed G was expressed as a percentage to represent the "wasted" potential for growth (O'Dor and Wells 1987).

Recent growth analysis

The 15 most recently deposited growth increments

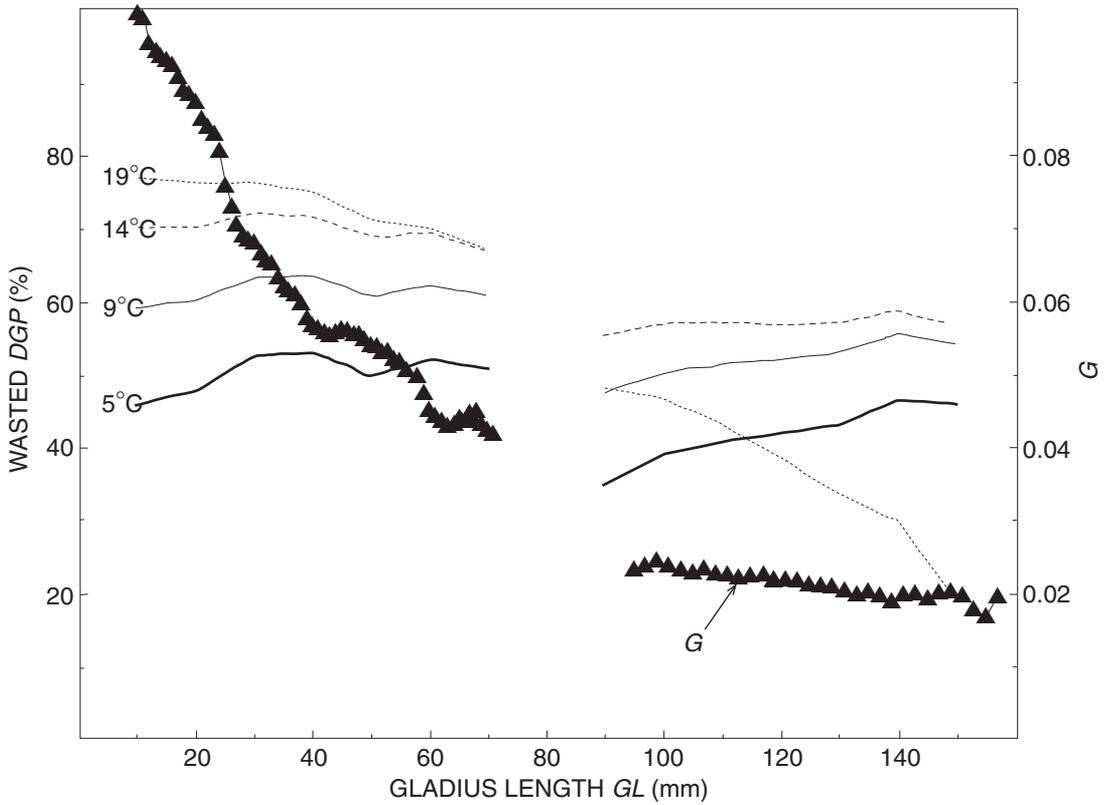


Fig. 2: Mean size-specific instantaneous growth rate G variation (filled triangles) and percentage waste of growth potential DGP at different temperatures. Temperatures in $^{\circ}\text{C}$ are indicated next to each line

were used to determine the recent growth index RGI of individual squid. A one-way analysis of variance (ANOVA) was employed to detect differences of mean GL among samples within each survey. When significant differences were found, a Tukey multiple comparison test was used to make isolated comparisons. The recent growth of the samples was compared using a one-way covariance analysis (ANCOVA) of repeated measures. This analysis tested for differences of mean RGI ("between subjects") and of mean recent growth profiles ("within subjects"; i.e. RGI considered as repeated measures within each squid gladius) among samples examined for each survey. Because growth increments tend to increase as a function of gladius length during the juvenile phase (Perez 1995), the "initial" gladius length back-calculated to 15 days before capture (GL_i), was used as covariate. A test for the interaction between SAMPLES and GL_i was carried out both between and within subjects (test of homogeneity of slopes) before each ANCOVA was performed. In

all surveys this interaction was found to be not significant within subjects (Table II). Between subjects, a marginal but significant difference was found among the slopes of the 1982 samples (Table II, $p = 0.039$). The ANCOVA was conducted on the samples of the 1982 survey as well. Tukey tests were also applied on the residuals of RGI regressed on GL_i . All hypotheses were tested at a 5% significance level.

The association of juvenile squid recent growth with the geographic distribution of the samples and environmental variables was investigated by an exploratory multivariate technique, Principal Components Analysis (PCA). The purpose of this technique is to reduce the number of dimensions of a multivariable set of observations allowing (a) identification of associations among the observations (grouping), and (b) detection of the main variables responsible for such associations. The geographical and environmental variables included were DSH, DGS, DSS, DNE, decimal latitude (LAT) and longitude (LONG), and

temperature *in situ* (TEMP, in °C). The variables representing recent growth of the samples were RES, the mean residuals of each sample obtained by the regression of *RGI* on GL_i , and RANK, the sample rank within its survey. All variables, except RANK, were standardized as a proportion of the mean. A correlation matrix was calculated for the standardized variables and new axes (factors) were extracted in the direction of greatest variance. These factors, which were essentially linear combinations of the original variables, were used to interpret association among samples.

RESULTS

General squid growth and oceanographic fronts: a bioenergetic approach

The changes in mean variation of instantaneous growth rate with increasing *GL* is shown in Figure 2 in relation to the size- and temperature-specific growth potential. The gap between 70 and 90 mm *GL* is due to the lower number of *GInc* available (and high variability) for that size interval. The objective of this analysis was to evaluate the effect of the thermal gradient across the Gulf Stream and shelf/slope front in the individual growth performance. Since *DGPs* are calculated for *ad libitum* food conditions, the wasted growth potential (expressed in percentage, Fig. 2) can also be thought of as being proportional to the quantity of food required to achieve maximum growth. Despite their faster growth rates, juveniles living in the Gulf Stream (temperatures >16°C) are food-limited, wasting around 80% of their growth potential. As juveniles move to colder slope waters their growth performance improves; wasted growth potential decreases to around 60%. In the shelf waters during spring (at 5 – 6°C), subadults (*GL* >100 mm) grow more slowly but are more efficient, wasting around 30 – 40% of their potential. Throughout summer, as squid grow and temperature increases on the shelf (Fig. 2), food-limitation increases.

Size-structure of samples and Recent Growth Analysis

Significant differences in the mean *GL* of the samples were found in all surveys ($p < 0.001$, Fig. 3). Samples of the 1981 survey were the most homogeneous in size and contained the smallest squid (Fig. 3b). Sharp size differences were characteristic among samples of the 1979 and 1989 surveys (Fig. 3a, e); the latter included the largest squid analysed in this study

(67.8 ± 12.8 mm and 80.3 ± 7.6 mm, mean \pm *SD* of samples 189 and 789 respectively). Initial size (GL_i) had a significant effect on *RGI* in all surveys (Between Subjects, Table II). As a consequence, because samples differed in size-structure, higher mean recent growth profiles observed in each survey corresponded to samples of larger squid.

The ANCOVA on recent growth increments revealed highly significant differences among samples of all surveys except that of 1979 (Between Subjects, source SAMPLE, Table II), where such differences were marginal ($p = 0.048$). Recent growth profiles (Within Subjects, source DAYS \times SAMPLE, Table II) were only significantly different among samples of the 1982 survey ($p = 0.029$). Pairwise comparisons, performed by the Tukey test on residuals of *RGI* regressed on GL_i (Fig. 3f–j), indicated results generally independent of the size structure of the samples (Fig. 3a–e). The analysis of residuals in samples of the 1982 survey produced inconclusive results (Fig. 3h) and was possibly affected by the different slopes (Table II).

Juvenile *Illex* recent growth condition and the environment

The analysis of principal components generated a bi-dimensional representation of the relationship between variables and samples (Fig. 4). The association among samples was analysed from the scores produced by the first two calculated factors that explained 66.5% of the total variance (Table III). Factor 1 was defined mainly by geographic and environmental components (higher positive and negative weighting, Fig. 4a, Table III). From the graphic representation in Figure 4, southern samples positioned close to the Gulf Stream boundary and collected at higher temperatures should be placed on the right hemiplane. Northern samples collected in cooler waters near the shelf, the shelf/slope front and the eddy activity should appear on the left hemiplane. Growth variables and longitude were particularly important in Factor 2 (Fig. 4a, Table III). Scored by this factor, eastern samples with relatively superior growth conditions would be plotted on the upper hemiplane and *vice versa*. The spatial representation of the samples scored by Factors 1 and 2 revealed a concentration of samples with superior growth conditions in the second quadrant (Fig. 4b). This pattern indicated that, within each survey, the squid with bigger recent growth increments tended to be (a) found in north-easterly samples, (b) collected in cooler waters near the shelf and the shelf/slope front, (c) under little influence of the Gulf Stream, but (d) possibly associated with Gulf Stream eddy activity. Samples 181 and 281, placed on the far right corner

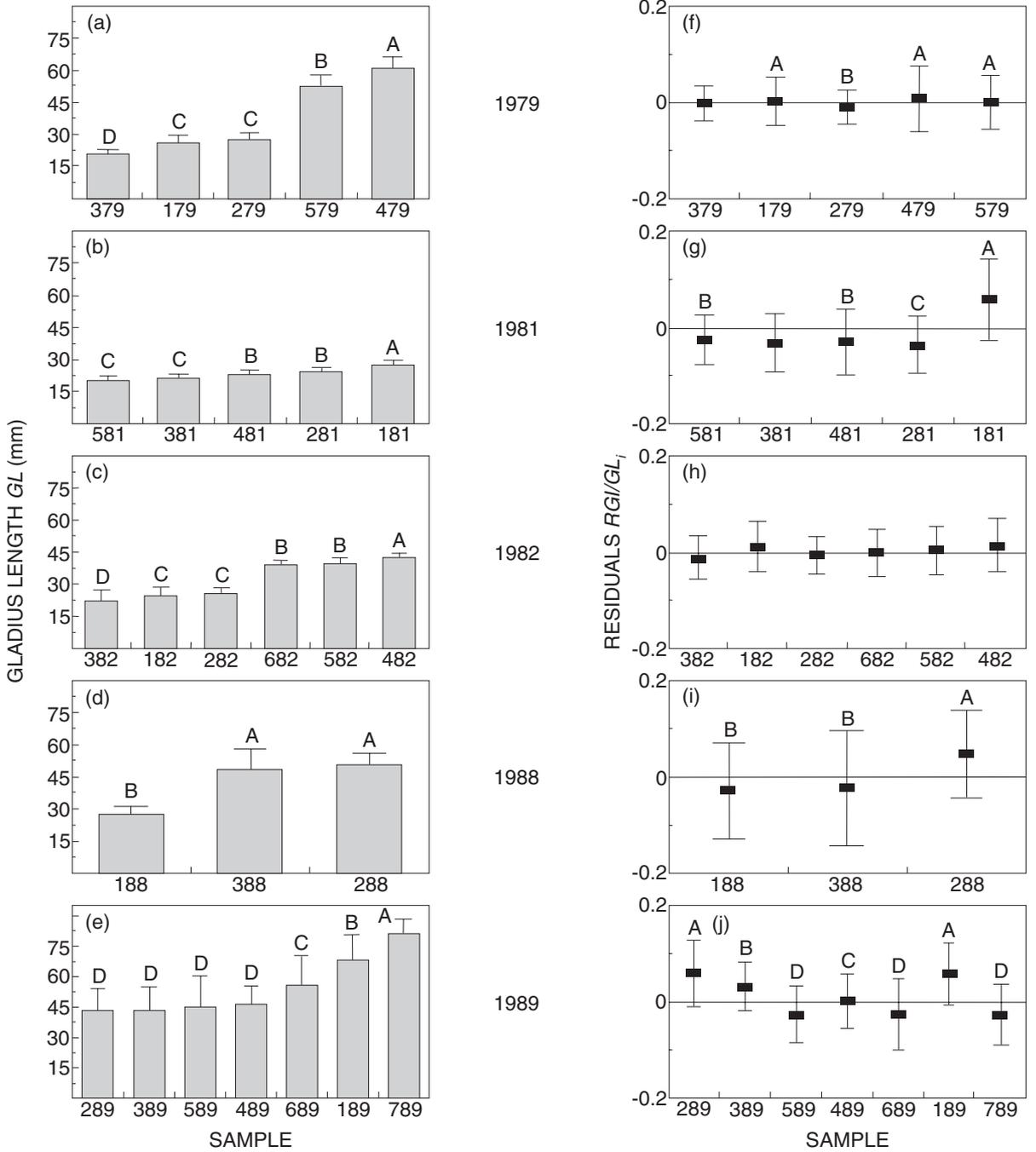


Fig. 3: Mean gladius length (a – e, histograms) and mean residual recent growth (f–j) of the samples analysed. Residuals were calculated from the regression of RG_i on GL_i . Samples are sorted from left to right in ascending order of mean gladius length. Error bars represent 1 SD. Capital letters above bars and symbols indicate the result of the Tukey test in descending order; samples labelled with the same letters were not significantly different. Samples not labelled could not be distinguished from the others by the test

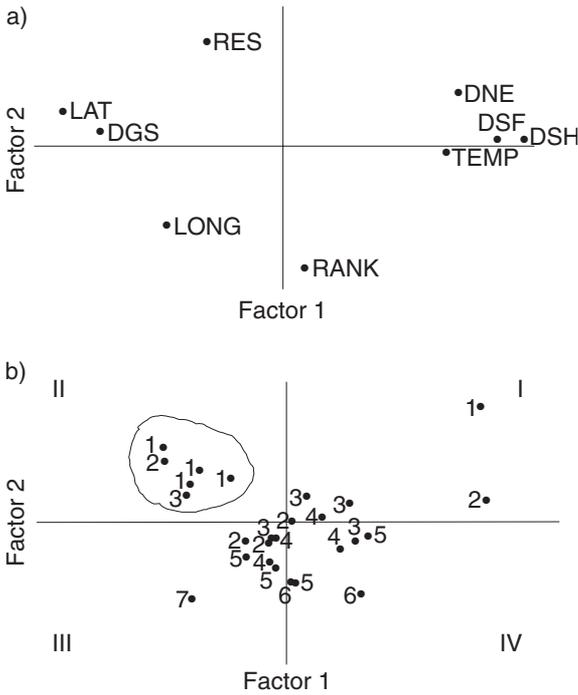


Fig. 4: Spatial representation of (a) geographic, environmental and growth variables and (b) of samples scored by the first two factors obtained from the Principal Components Analysis. Factor 1 (horizontal axis) explained 46.4% of the variance and Factor 2 (vertical axis) explained 20%. In (b), samples are labelled by their ranks within each survey. The group marked were mainly samples with faster growth. Roman numbers indicate the four quadrants

of the first quadrant, diverged from the main pattern. In spite of its fast growth and the eastern position (the easternmost of all samples analysed), 181 was collected offshore of the Gulf Stream boundary at a great distance from the shelf.

DISCUSSION

Somatic growth, the result of energetic interactions and determinant of an organism's size at any time, measures an individual's performance under environmental influences. As shown for captive *I. illecebrosus* (Perez *et al.* 1996) and *Sthenoteuthis oualaniensis* (Bizikov 1995), variation in the gladius increment width reflects somatic growth and is sensitive to feeding events and temperature fluctuations. In this study, series of growth increments recently deposited

Table III: Principal Components Analysis employed to evaluate the association between growth, the horizontal distribution of juveniles and the main oceanographic features. Variables included are temperature °C (TEMP), decimal latitudes (LAT) and longitudes (LONG), distances (in km) from the shelf break (DSH), the Gulf Stream boundary (DGS), the shelf/slope front (DSF) and the nearest eddy (DNE), residuals of the regression $RGI \times GL_i$ (RES), and the growth rank of each sample within its survey (RANK). Values shown for all variables are unstandardized. The linear coefficients of the variables in the first five factors rotated by the PCA are indicated. The eigenvalues and the variance explained by each factor, including the first two used for the analysis, are indicated in the last two rows

Component	Factor				
	1	2	3	4	5
DSH	0.962	0.503	-0.078	0.004	-0.160
DGS	-0.272	0.112	0.121	0.581	0.078
DSF	0.856	0.052	0.207	-0.205	0.128
DNE	0.697	0.384	-0.360	0.378	0.076
TEMP	0.652	-0.031	0.584	0.310	0.253
LAT	-0.877	0.246	-0.336	-0.038	0.156
LONG	-0.461	-0.551	0.641	0.014	-0.118
RES	-0.304	0.743	0.369	-0.366	0.213
RANK	0.088	-0.849	-0.352	-0.117	0.341
Eigenvalue	4.179	1.805	1.318	0.769	0.317
Variance explained (%)	46.43	20.05	14.64	8.54	3.53

on the gladius of juvenile *I. illecebrosus* showed clear variability associated with individual response to environmental gradients experienced during the migration across the Gulf Stream/ slope water front system. The analysis provided an insight into the constraints and advantages of such migration.

Squid growth is greatly enhanced as temperature and food ration increase (O'Dor *et al.* 1980, Forsythe and van Heukelem 1987). Fastest growth conditions, therefore, should be associated with an environment where both factors are maximized. During the inshore migration, however, juvenile *Illex* will rarely experience such an environment. Instead, the transition from the Gulf Stream to slope and coastal water during spring represents a nearly 20°C decrease in environmental temperature, while providing access to an environment approximately 4 – 12 times richer in phytoplankton and 3 – 4 times richer in zooplankton than the Gulf Stream (Raymont 1980, 1983, Allison and Wishner 1986). Comparison of gladius growth increments and size- and temperature-specific potential growth suggests that early life movement across water masses may represent a trade-off between favourable temperatures in the Gulf Stream and favourable food availability in slope and coastal waters. In the warm waters of the Gulf Stream, where embryonic development and hatching are most likely to take place (Trites 1983,

O'Dor and Balch 1985, O'Dor *et al.* 1986), the potential for growth is high but mostly wasted, possibly because of food-limitation. Moving towards colder slope water substantially decreases metabolic costs and feeding rates. Although the potential for growth is reduced, the cost of living is lower, allowing a potential scope for growth rate to increase. A similar pattern has been conceptually shown by Brandt (1993), who used an energetic model to assess growth responses of fish larvae to temperature and food gradients across fronts.

Growth during early life is expected when the energy gained in one meal exceeds the energy required to find and obtain the next one. As young *Illex* exhibit limited swimming capacity which is energetically expensive (O'Dor *et al.* 1986), fast growth probably requires food resources to be quite concentrated. Entrainment in the slope water during spring provides access to a generally food-enriched environment, but advantageous concentrations of food particles seem also to occur mainly (a) at the interfaces with the Gulf Stream and the coastal water and (b) associated with circulation features of the Gulf Stream, such as meanders, eddies and warm-core rings (Fournier 1978, Herman *et al.* 1981, Olson 1986, Arnone *et al.* 1990, Mann and Lazier 1991, Bakun and Csirke 1998). The general pattern emerging from analysis of gladius recent growth suggests that juvenile growth is improved shorewards as squid abandon the Gulf Stream and approach the shelf/slope front. Although this pattern seems to reflect the increased plankton abundance on the shelf break, it also appears to contradict the hypothesized importance of the Gulf Stream boundary as a barrier. Two factors may be associated with such contradiction:

- (i) it is possible that diffusion processes related to the meander activity may eject juveniles from the front (Bakun and Csirke 1998);
- (ii) the environment may be particularly advantageous during paralarval stages – juveniles, with better swimming capabilities, would be able to encounter other concentrations of food, closer to the adult habitat, perhaps at the shelf/slope front.

The exceptional growth exhibited by the squid of the 1981 survey near the boundary of the Gulf Stream (in particular in Sample 181) provides some support for a combination of both factors. First, owing to the small size of the individuals, paralarval growth was better addressed in those samples than in any other sample considered for this study. Second, the samples originated from the easternmost area. Considering that transport in the Gulf Stream is eastwards, that would indicate that somehow those squid were retained in the Gulf Stream, near the front. In consequence, unlike juveniles from other surveys, their

faster recent growth could be explained by favourable food concentrations and higher temperature at the Gulf Stream boundary.

After entrainment in the slope water, growth seemed to be enhanced north-easterly, which likely reflects the patterns of circulation of the Gulf Stream and the slope water. As the Gulf Stream detaches from the shelf and turns eastwards, meandering and eddy activity increase and young *Illex* are ejected into the slope waters (Rowell and Trites 1985). The seaward boundary of the slope water splits off the Gulf Stream and flows north-east (Csanady and Hamilton 1988), probably transporting entrained *Illex* to the shelf/slope front, where growth may have been favoured.

Squid with faster growth in each survey were also found relatively close to warm-core rings. Whether this association reflects previous transport (Hatanaka *et al.* 1985) or the enriched environment formed at the ring periphery (Olson 1986) is unclear.

In summary, access to food seems to be a limiting factor shaping the early life history of *I. illecebrosus*. Onshore migrations are driven by the elevated feeding requirements and involve adaptations of metabolic patterns to compensate for decreasing temperatures. These adaptations have been predicted by poikilotherm bioenergetic models (Brett 1979, O'Dor and Wells 1987, Brandt 1993). Furthermore, processes of surface and subsurface transport may be important factors responsible for the "delivery" of these juveniles to areas of particular food concentration and their retention there. Transport of *Illex* offspring by the Gulf Stream towards the feeding grounds has been compared to a "one-way train" (Bakun and Csirke 1998). Individuals may "fall off the train" at any point along the trajectory, depending on the intensity of the meandering and the eddy activity (Rowell and Trites 1985). Entrained off the Scotian Shelf, juveniles can be transported north-eastwards towards areas of food concentration at the shelf break. Retained at the Gulf Stream boundary, juveniles may be transported eastwards while benefiting from a favourable concentration of food at the front. In such circumstances, entrainment into the adult habitat may be even more advantageous because it would occur in the highly productive water of the Grand Banks system (Mann and Lazier 1991, Prasad and Haedrich 1993). In fact, *Illex* recruited to the inshore area off Newfoundland are considerably larger when young than those in other southern areas (Morris and Aldrich 1985, Dawe and Beck 1997), a feature that suggests fast growth during early life.

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