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THE EARLY LIFE HISTORY OF THE SHORT-FINNED SQUID, *Illex illecebrosus*
(CEPHALOPODA : OMMASTREPHIDAE), AS RECONSTRUCTED FROM THE
GLADIUS STRUCTURE.

by

José Angel Alvarez Perez

Submitted in partial fulfillment of the requirements for the degree of Doctor of
Philosophy

at

Dalhousie University

Halifax, Nova Scotia

December, 1994

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*This thesis is dedicated to the memory of Maria Antonia Perez
Jaldón (1900-1995)*

TABLE OF CONTENTS

List of tables	viii
List of figures	ix
Abstract	xii
List of abbreviations and symbols	xiii
Acknowledgements	xiv
 Chapter 1. General Introduction	 1
1.1. Fishery and Life-cycle	4
1.2. Reconstruction and analysis of individual growth histories: the approach.	9
1.3. Objectives	12
 Chapter 2. Evaluation of Gladius Structure for Age and Growth Studies of the Short-Finned Squid, <i>Illex illecebrosus</i>.	 15
2.1. Introduction	15
2.2. Material and Methods	16
2.2.1. Gladius analysis	16
2.2.2. Statolith analysis	19
2.3. Results	19
2.3.1. Relationship between gladius and somatic growth	19
2.3.2. Gladius morphology and growth increments	23
2.3.3. Growth increment interpretation	26
2.3.4. Reconstruction of mean growth trajectory	30
2.3.5. Reconstruction of gladius growth histories	30
2.4. Discussion	35
 Chapter 3. Critical Transitions in Early Growth Histories of <i>Illex illecebrosus</i> Reconstructed from the Gladius	 40

3.1. Introduction	40
3.2. Material and Methods	41
3.2.1. Gladius analysis and numerical representation of growth	42
3.2.2. Growth analysis	46
3.2.3. Morphometric analysis	47
3.3. Results	47
3.3.1. Changes in body form	47
3.3.2. Early growth history reconstruction	50
3.3.3. Development of sexual characters	50
3.3.4. Environment transitions	53
3.4. Discussion	53

Chapter 4. Small-scale Horizontal Variation in the growth of Juvenile *Illex*

<i>illecebrosus</i>	59
4.1 Introduction	59
4.2. Material and Methods	60
4.2.1. Origin of samples and environmental data	60
4.2.2. Recent growth analysis	63
4.3. Results	64
4.3.1. Size-structure of samples and recent growth analysis	64
4.3.2. Spatial distribution and main environmental features in relation with juvenile <i>Illex</i> recent growth condition.	65
4.5 Discussion	75

Chapter 5- Seasonal, Interannual and Geographic Variability in the Juvenile

Growth of <i>Illex illecebrosus</i>	85
5.1. Introduction	85
5.2. Material and Methods	86
5.2.1. Samples	86
5.2.2. Gladius growth and data analysis	88

5.3. Results	88
5.3.1. Seasonal variability	88
5.3.2. Interannual variability	91
5.3.4. Geographic variability	94
5.4. Discussion	94
 Chapter 6 - General discussion and conclusions	 104
 Appendix 1	 110
Appendix 2	112
Appendix 3	116
Appendix 4	118
Appendix 5	123
Appendix 6	126
Appendix 7	129
 References	 135

LIST OF TABLES

Table 2.1.	Linear regression coefficients of the relationships Gladius Length vs. Mantle Length and Gladius Length vs. Log-transformed Weight.. . .	20
Table 2.2.	Number of growth mark and mean increment width per 10 mm of gladius length intervals.	27
Table 2.3.	Results of the test for consistency of gladius growth marks counts..	28
Table 2.4.	Comparison between gladius increments and daily size-specific growth rates (mm/d) reported in the literature	38
Table 3.1.	Ontogenetic allometry between Log GL and the Log transformed: AILL, ED, HW and FL in juvenile <i>Illex illecebrosus</i>	45
Table 3.2.	Linear regressions of GInc on GL and test for the effect of sex differentiation in size-specific growth (ANCOVA).	49
Table 4.1.	Comparison of juvenile <i>Illex illecebrosus</i> recent growth in five surveys off the Scotian shelf (ANCOVA)..	66
Table 4.2	Analysis of principal components on the association between growth, horizontal distribution of juveniles and main oceanographic features..	78
Table 5.1.	Gladius growth increments variation of all squid groups analyzed..	89
Table 5.2.	Seasonal, interannual and geographic comparisons of the total recent growth measured on the gladius of juvenile <i>Illex illecebrosus</i> (ANCOVA).	92

LIST OF FIGURES

Figure 1.1.	Morphological changes during early life growth of <i>Illex argentinus</i> .	3
Figure 1.2.	Schematic life cycle of <i>Illex illecebrosus</i> in the Northwest Atlantic.	5
Figure 1.3.	Annual catches of <i>Illex illecebrosus</i> in the Northwest Atlantic.	7
Figure 1.4.	Schematic representation of the early life ecology of <i>Illex illecebrosus</i> including life-style transitions and the penetration into the subadult coastal habitat.	8
Figure 1.5.	Schematic view of an individual specific growth rate series reconstructed from gladius analysis.	11
Figure 2.1.	Schematic dorsal view of <i>Illex illecebrosus</i> gladius and position in relation to the squid mantle.	17
Figure 2.2.	Relationship between ML and GL.	21
Figure 2.3.	Relationship between total wet W and GL.	22
Figure 2.4.	Accretive growth of the ostracum layer on the gladius of <i>Illex illecebrosus</i>	24
Figure 2.5.	Scanning Electron Micrographs of the dorsal gladius structure of an <i>Illex illecebrosus</i> paralarva.	25
Figure 2.6.	Relationship between the number of statolith growth increments and the number of gladius growth increments anterior to 100 mm GL.	29
Figure 2.7.	Growth curves reconstructed from gladius analysis.	31
Figure 2.8.	Reconstructed individual gladius growth series of three captive squids.	32
Figure 2.9.	Pattern of estimated cross-correlation between the water temperature differenced series moved over the gladius growth series of the female ROR.	34
Figure 3.1.	Dorsal view of juvenile <i>Illex illecebrosus</i> including the position of the gladius and the body measurements.	43
Figure 3.2.	Variation of size- and temperature-specific daily growth potential as estimated by the energetic budget equation.	44
Figure 3.3.	Ontogenetic allometry between Log GL and the Log-transformed body	

	proportions in juvenile <i>Illex illecebrosus</i>	48
Figure 3.4.	Mean size-specific growth curve reconstructed from the gladius analysis of <i>Illex illecebrosus</i>	51
Figure 3.5.	Mean size-specific growth curves reconstructed from the gladius analysis of males and females <i>Illex illecebrosus</i>	52
Figure 3.6.	Mean size-specific instantaneous growth rate variation and percentile waste of growth potential at different temperatures.	54
Figure 4.1.	Study area and locations where juvenile <i>Illex illecebrosus</i> were sampled in relation to the northern boundary of the Gulf Stream, the shelf/slope front and the Gulf Stream eddy activity	62
Figure 4.2.	Mean gladius length and mean residual recent growth of the analyzed samples.	67
Figure 4.3.	Mean recent growth profiles of the analyzed squid samples as reconstructed from the gladius structure.	69
Figure 4.4.	Positions where the analyzed samples were collected in the 1979 survey in relation to the nearest available daily positions of the boundary of the Gulf Stream, the shelf/slope front and warm-core rings.	71
Figure 4.5.	Locations where the analyzed samples were collected in the 1981 survey in relation to the nearest available daily positions of the boundary of the Gulf Stream, the shelf/slope front and warm-core rings.	72
Figure 4.6.	Locations where the analyzed samples were collected in the 1982 survey in relation to the nearest available daily positions of the boundary of the Gulf Stream, the shelf/slope front and warm-core rings.	74
Figure 4.7.	Locations where the analyzed samples were collected in the 1988 survey in relation to the nearest available daily positions of the boundary of the Gulf Stream, the shelf/slope front and warm-core rings.	75
Figure 4.8.	Locations where the analyzed samples were collected in the 1989 survey in relation to the nearest available daily positions of the boundary of the Gulf Stream, the shelf/slope front and warm-core rings.	76
Figure 4.9.	Analysis of Principal Components. Spatial representation of geographic,	

	environmental and growth variables, and samples scored by the first two factors.	80
Figure 5.1.	Size-specific variation of gladius growth increments measured in squids caught in April, June and August 1989.	90
Figure 5.2.	Size-specific variation of gladius growth increments measured in squids caught in late summer-spring of 1979, 1981, 1982, 1988 and 1989.	93
Figure 5.3.	Mean residuals of the total recent growth in the seasonal, interannual and geographic analysis.	95
Figure 5.4.	Size-specific variation of gladius growth increments measured in squids caught in January 1985 between Cape Hatteras and Florida in comparison with the northern areas.	96
Figure 5.5.	Relationships between interannual patterns of recent growth, ranked abundances of <i>I. illecebrosus</i> and major environmental fluctuations.	98
Figure 6.1.	Mean growth residuals of squids caught in the 1979 survey in relation to the distribution of chlorophyll concentration along a N-S transect (64° W).	107

ABSTRACT

The annual populations of the short-finned squid, *Illex illecebrosus*, are spawned throughout the year south of Cape Hatteras (35°S), and recruit in different places along the eastern coast of North America. The early life, a critical period for survival and recruitment, is spent in the meandering Gulf Stream/ Slope Water front where offspring increase a hundred fold in length, change from a planktonic to a nektonic adult life-style and experience a decrease in environmental temperature of as much as 20°C. Growth during this phase was reconstructed from periodic growth marks deposited on the gladius. The main objectives were to investigate the variability of juvenile growth in relation to life history events, oceanographic structure, geographic distribution and seasonal and interannual fluctuations of the environment. The juvenile/offshore growth phase was exponential. A change to linear growth occurred after the adult/onshore life-style was attained (GL > 80-90 mm). During the juvenile life, a major change in body shape and a separation between two size-specific growth phases was associated with the transition from the macroplanktonic to micronektonic habitats (30-40 mm GL). Sexual growth differences occurred among subadults (GL > 120 mm) prior to the onset of maturation. Juvenile growth conditions improved as squids moved from the Gulf Stream to colder and food-enriched Slope Waters. In these conditions metabolic costs decreased and more food became available. In the Slope Water off the Scotian Shelf, growth was enhanced shoreward and particularly in proximity to the shelf/slope front. The access to and retention of individuals in these favourable areas were related to processes of transport in the Gulf Stream and Slope Water. Growth conditions of juveniles were enhanced during spring probably as a consequence of the seasonal peak of biological production off Nova Scotia. Interannual variations of the environment here were not consistently detected in the gladius growth variability suggesting that patchy production plays a role in recruitment regulation. Southwards, near the spawning grounds, juvenile growth of *Illex* sp. was much slower contradicting laboratory studies indicating faster growth in tropical cephalopods due to positive effects of high temperatures. The results of this study emphasized the potential of the gladius technique for squid growth history reconstruction, and provided empirical evidence for hypothesized ecological processes acting during early life of *Illex* and other pelagic squids.

LIST OF ABBREVIATIONS AND SYMBOLS

<u>Abbreviation</u>	<u>Meaning</u>
Å	Angstrom
α	alpha, significance level
c.i.	confidence interval
CV	coefficient of variation
df	degrees of freedom
F	F statistic
g	gram
m	meter
mm	millimetre
MS	mean square
n	sample size
p	probability
‰ or ppt	parts per thousand
r^2	coefficient of determination
SD	standard deviation
SE	standard error
t	t-statistics

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CHAPTER 1. General Introduction

Pelagic squids of the family Ommastrephidae sustain the world's most important cephalopod fisheries. Between 1979 and 1982, only six species of this family comprised over 50% of the total reported cephalopod catches (204,052 - 482,073 metric tones; FAO statistics in Ratjhen and Voss 1987). In recent years, some of these particularly abundant populations have collapsed or shown irregular fluctuations (Coelho 1985; Hatanaka et al. 1985a; Hatanaka et al. 1993). As understanding of the mechanisms that regulate squid populations is now urgently required, major efforts have been made to this end (Okutani et al. 1993; Rodhouse et al. in press).

Like many cephalopods, ommastrephid squids are short-lived, semelpareous, annual species (Boyle 1983 for review); individual reproductive effort is concentrated in one spawning period and the replacement of the entire population depends on the reproductive success of each generation. The processes of recruitment, which link successive generations, regulate population abundance and may explain its variations (Amaratunga 1983; Amaratunga 1987).

Recruitment may be largely affected by important intergenerational losses of individuals occurring during the early planktonic life stage (Amaratunga 1987). The processes involved in such losses, however, have not been empirically addressed in squids but, instead, are mostly hypothesized from patterns established for other marine populations with complex life cycles (Strathmann 1985; Sinclair 1987; Roughgarden et al. 1988; Rumrill 1990; Vecchione 1991; Bakun and Csirke in press). Squid paralarvae¹ are difficult to raise in captivity. In nature, sampling methods seem to be inadequate and the taxonomy sometimes ambiguous (Vecchione 1987). Although innovative approaches have progressively overcome current methodological limitations (Vecchione 1988; Vecchione 1991; Sweeney et al. 1992; Bigelow 1992; Bigelow and Landgraf 1993), most of the questions about the early life ecology of squids still remain unanswered. The

¹Paralarva is the general term which defines the planktonic young of cephalopods. It was introduced by Young and Harman (1988) in order to replace the broadly used "larva" which is not appropriate to this group

compilation of available information on the functional morphology, behaviour and distribution of cephalopod early life stages, have allowed some inferences to be made about potential ecological pressures (Boletzky 1987; Okutani 1987; Vecchione 1987; Vecchione 1991):

a.) From hatching, squid paralarvae are highly mobile and well "equipped" for external feeding and predator avoidance (Fig. 1.1). Morphologically, most species have a developed central nervous system, large eyes, ciliary receptor systems, raptorial apparatus (arms, tentacles, suckers), buccal mass with beaks and radula, functional salivary glands and digestive system, propulsive mantle and funnel, and an ink sac (Boletzky 1987). The energetic maintenance of this active stage, however, is costly and the limited internal yolk reserves may be depleted in a few days (O'Dor et al. 1986). Since external feeding is required shortly after hatching, risks of starvation may be significant (Vecchione 1991).

b.) For many species the attainment of the adult life-style involves a descent from the planktonic epipelagic to the nektonic meso- and bathypelagic environments (Vecchione 1987) over a range of sizes greatly exceeding that of fish (O'Dor and Webber 1986). Although squids never undergo a radical metamorphosis (Okutani 1987; Boletzky 1987), discontinuous changes in the general form of the body and the transformation of some particular structures (e.g. tentacles; Fig 1.1) normally occur in adaptation to hydrodynamic constraints and the availability of different prey (Nesis 1979a; Okutani 1987; Vecchione 1987; Sweeney et al. 1992; Vidal 1994a). The inability to adapt promptly to new niches may lead to periods of fasting and impose limitations for survival (Nesis 1979a).

c.) In theory, zooplankters the size of squid paralarva are particularly vulnerable to predation risks. However, since paralarvae are scarce in the plankton in comparison with similar-sized organisms (e.g. copepods), mobile, and highly "perceptive" of their environments (see morphological adaptations above), predation may be relatively less significant (Vecchione 1987).

d.) The environment appears to be an important influence on most ecological

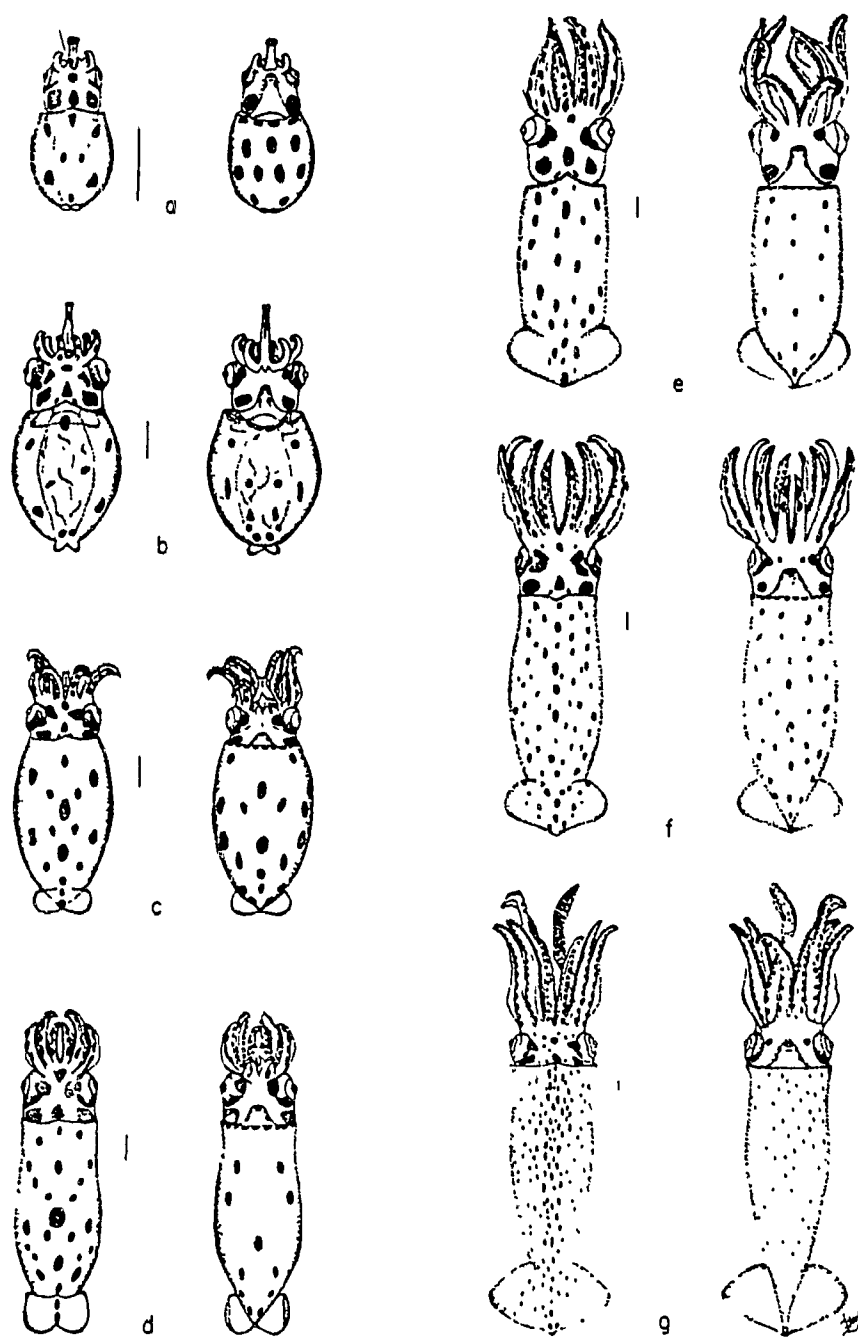


Figure 1.1. Morphological changes during early life growth of *Illex argentinus* (dorsal and ventral views). a. 1.4 mm ML; b. 3.5 mm ML; c. 6.0 mm ML; d. 8.0 mm ML; e. 11.0 mm ML; f. 15.0 mm ML; g. 30.0 mm ML. Scale bars = 1.0 mm. Reproduced from Vidal (1994).

pressures suggested above (Bakun and Csirke in press). Abundant populations, particularly in some ommastrephids (e.g. species of the genus *Illex* and *Todarodes*), have life cycles that are adapted to permanent oceanographic systems that normally include high-velocity geostrophic currents (Hatanaka et al. 1985a; Coelho 1985). Physical processes associated with such systems affect paralarval ecology in different ways: (1) they induce trophic enrichment and the concentration of food particles in current boundary zones (Fig. 1.2); growth and survival, particularly during critical transitional periods, may be enhanced in such areas (Bakun and Csirke in press); (2) they provide transport and retention of paralarvae in favourable areas for reproduction (Rowell and Trites 1985); and (3) they exhibit important thermal gradients that may greatly affect metabolic and feeding rates and set energetic boundaries for growth and starvation (O'Dor and Wells 1987). The effect of environmental variability on ecological processes during early life has been regarded as essential for understanding the mechanisms of recruitment in squids and other cephalopods (Anon. 1987; Anon. 1994; Bakun and Csirke in press).

Based on this framework, the present study provides a new view of the early life ecology of the northwest Atlantic short-finned squid *Illex illecebrosus*, one of the most abundant and unpredictable cephalopod resources of the world (Coelho 1985), as an example of the application of a powerful new technique. Brief descriptions of the fisheries and life cycle, the approach and objectives of this study follow.

1.1. Fishery and Life-cycle

The geographical distribution of *I. Illecebrosus* ranges from south Florida to Greenland (Roper et al. 1983). Important concentrations typically occur during summer and autumn from the Gulf of Maine to Newfoundland, and have sustained a valuable although highly unpredictable fishery. Historically, a local squid jigging fishery existed from the late 1800's off Newfoundland primarily to supply the bait for the cod fishery. From 1964 and through the 1970's, attracted by an expanding international market, distant-water fleets from countries such as the USSR, Japan and Spain, entered the fishery

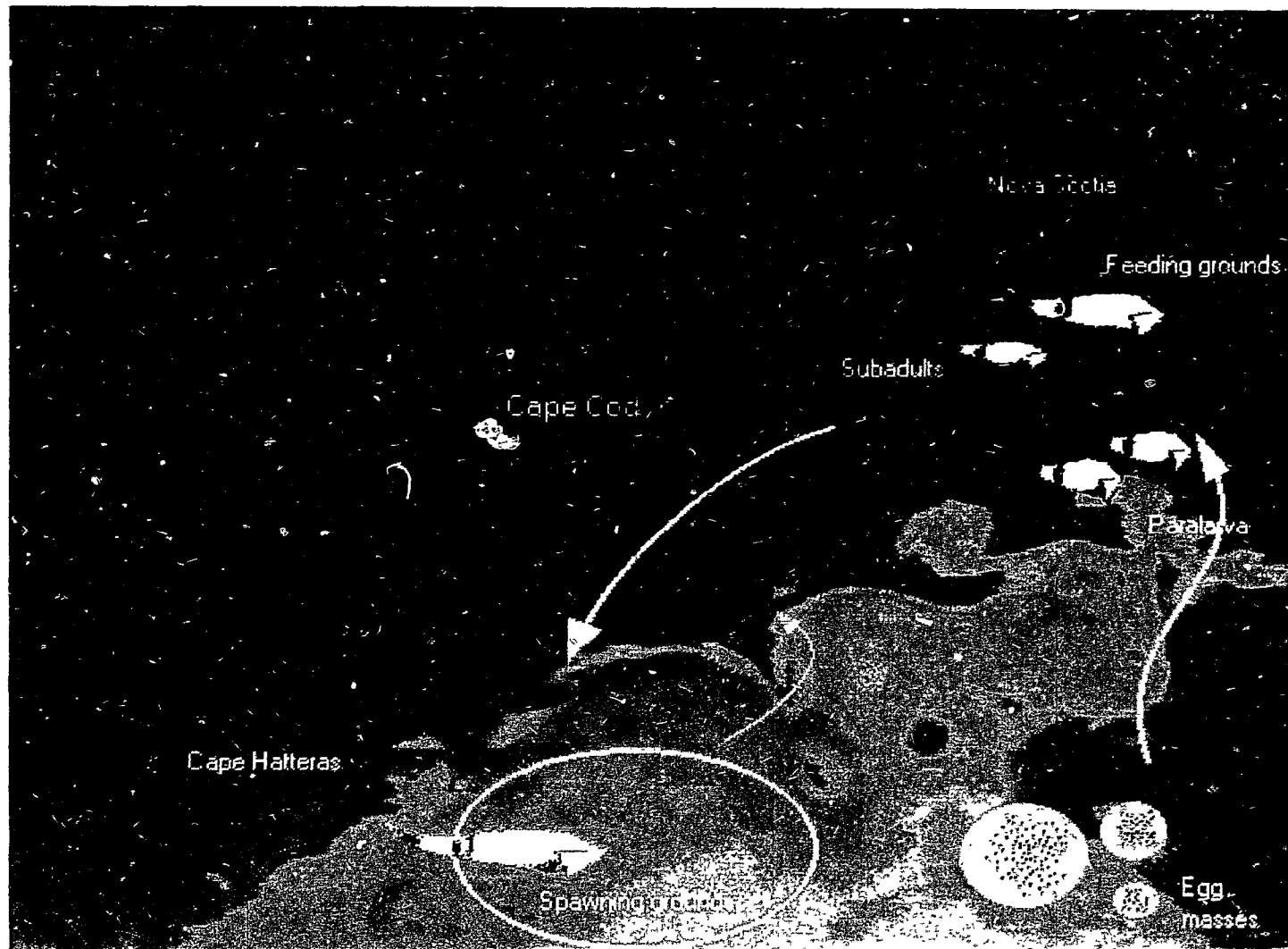


Figure 1.2. Life cycle of *Illex illecebrosus* in the Northwest Atlantic.

using bottom and mid-water trawling and jigging (Lange and Sissewine 1981). During this period nominal catches in the northwest Atlantic increased by a factor of 60, reaching a peak in 1979, with more than 170,000 tons reported (Black et al. 1991; O'Dor and Dawe in press). The fishery rapidly collapsed to non-commercial levels after that and has not recovered (Fig. 1.3).

During the late 70's and 80's, intense efforts were directed towards understanding the *Illex* life cycle and population biology. These included both field and laboratory studies (see O'Dor 1983; Black et al. 1991 for reviews). The life cycle of *I. illecebrosus* rarely extends beyond one year, includes long spawning migrations, and utilizes the geostrophic transport of the Gulf Stream. Spawning occurs throughout the year presumably south of Cape Hatteras (Fig. 1.2). Fertilized females produce around 400,000 eggs that are enclosed in jelly egg masses, about 0.5 - 1.0 m in diameter. In contact with the Gulf Stream, these egg masses become neutrally buoyant and are transported northwards while the embryonic development is accelerated. Within 9 to 16 days, free-swimming paralarvae, approximately 1.0 mm long, hatch and concentrate in the near surface layers at the inshore boundary of the Gulf Stream (Fig. 1.2 and 1.4). Since they are provided with a limited yolk supply, unfed paralarvae starve around five days after hatching, and may depend on high food availability to meet their elevated metabolic costs and required growth rates (O'Dor et al. 1986). Paralarvae are entrained in the Slope Water and, 3-4 months later, recruits, around 100 mm (mantle length), reach the continental shelf and assume the nektonic, schooling adult life-style (Fig. 1.2 and 1.4). Feeding and growth are intensified during this period. As squid increase in size, they switch their main prey from crustaceans to pelagic fish. Cannibalism arises when prey are not available and represents a substantial source of food and natural mortality, especially towards the end of the feeding season (Amaratunga 1983; Maurer and Bowman 1985). Females grow faster, attain larger sizes and mature later than males. Males accumulate spermatophores that are transferred to the mantle cavity of females during the brief copulation. Maturing females carry spermatophores attached to the mantle wall near the base of their gills and oviducts. With the onset of maturation, both males and females emigrate to the southern spawning grounds and they die after spawning.

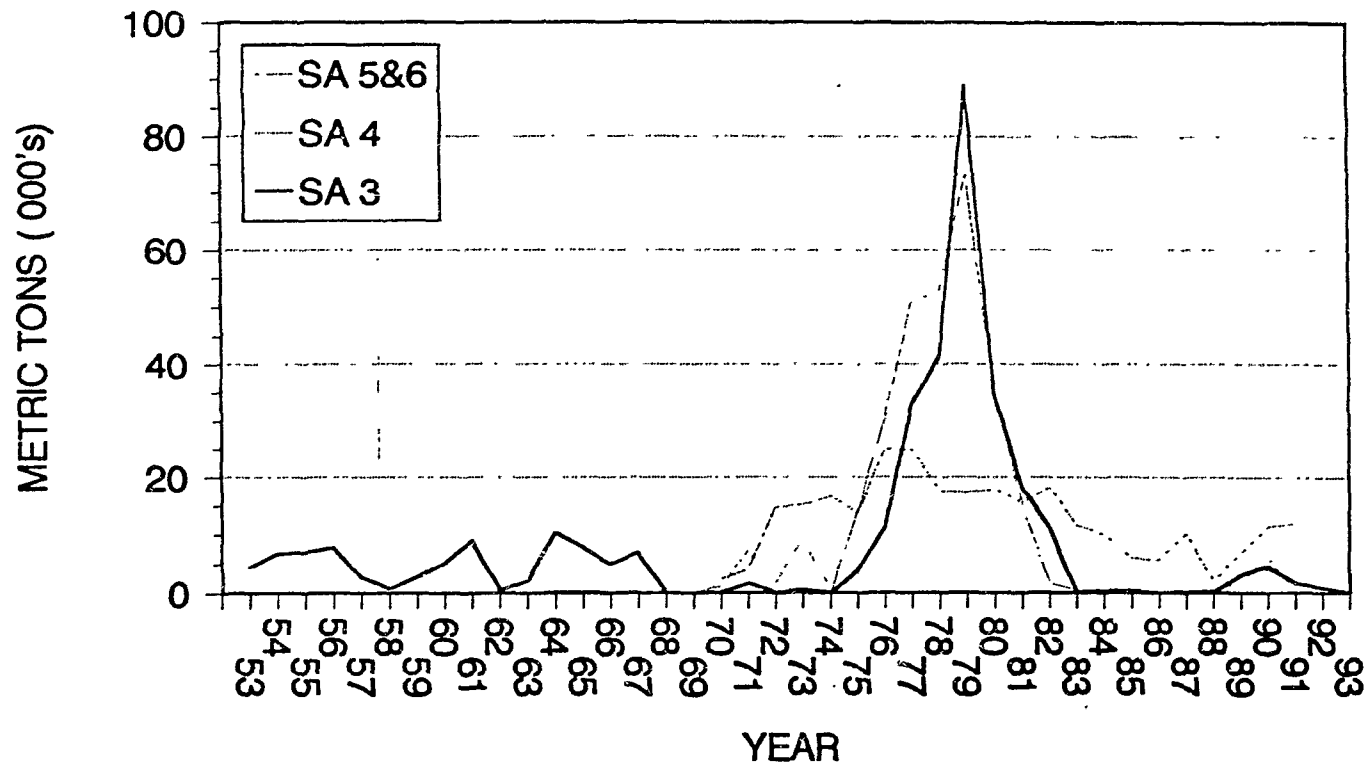


Figure 1.3. Annual catches of *Illex illecebrosus* in the Northwest Atlantic between 1953 and 1993 for NAFO subareas 3,4, 5 and 6.

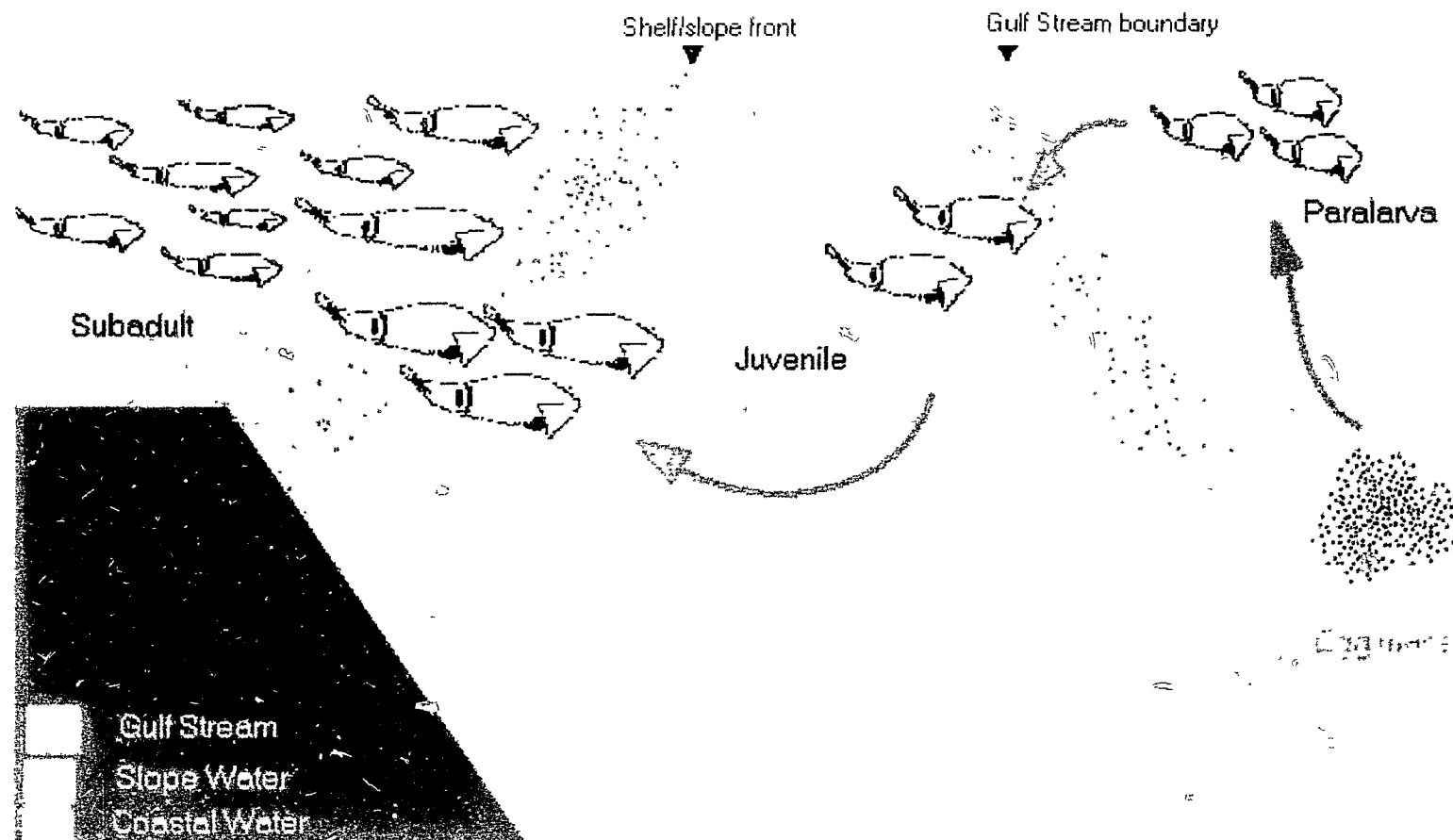


Figure 1.4. Schematic representation of the early life ecology of *Illex illecebrosus* including life-style transitions and the penetration into the subadult coastal habitat.

Some life history traits such as size-at-maturity and fecundity, as well as the timing and location of life cycle events, may vary significantly in association with the diversified population structure (Coelho and O'Dor 1993, Coelho et al. 1994). The most abundant and best studied population component derives from winter spawning events, and reaches the Scotian Shelf and inshore Newfoundland during spring and summer. On these feeding grounds, individuals grow from approximately 100 to 250-300 mm ML and emigrate to the spawning grounds in October-November. Minor and less-studied population components occur at different times of the year along the coast of the United States. In recent years it has been suggested that mechanisms of *Illex* population regulation may be largely related to the population diversity, selection on life-history traits, and the gene flow among the different population components (O'Dor 1992; O'Dor and Coelho 1993, Coelho et al. 1994).

1.2. Reconstruction and analysis of Individual Growth Histories: the Approach.

The early life ecology of *I. illecebrosus* was investigated from the historical growth of an internal skeletal structure, the gladius or pen. This approach is analogous with the reconstruction of tree ring growth chronologies (Fritts 1976) and has been widely used with the skeleton, or skeletal structures of various aquatic organisms including: bivalve and barnacle shells, colonial coral skeletons, polychaete jaws, and larval fish otoliths (Roads and Lutz 1980; Campana and Jones 1992). In general, it is based on the fact that physiological processes and environmental fluctuations are recorded in the patterns of skeletal growth. Thus when growth chronologies are reconstructed, the variability of internal processes and external conditions acting upon the individual, can be assessed historically. In sessile organisms, this approach has been often used to reconstruct past environmental conditions (Roads and Lutz 1980). In mobile organisms, such as fish larvae, applications in population ecology have been developed based on the back-calculation of individual growth rates (Campana and Jones 1992).

Growth, as the result of energetic interactions and determinant of the individual size at any one time, measures an individual's performance under environmental

influences. A series of periodic growth increments that describe the Individual Growth History (IGH) of an animal in the sea is, in theory, a continuous approximation of the dynamics of such performances. Individual growth histories can be reconstructed from the periodic accretive growth of a skeletal structure if the deposition of skeletal material is proportional to somatic growth (Campana and Neilson 1985). If this requirement is satisfied, the estimated IGH contains the cumulative variability introduced by the effect of various components affecting growth (Fig.1.5):

$$G_{it} = M_{it} + A_{it} + e_{it} \quad (1.1)$$

The specific growth rate (G) of an individual (i) at anyone time interval (t) results from the additive effect of: an error component, e ; a mean component, M , generally size-dependent and taken as constant for all individuals; and an individual component, A , which comprises the sources of growth variability intrinsic to the i^{th} individual including: individual phenotypic features, food availability and fluctuations of the physical environment. The analysis of an IGH consists of discriminating and attempting to identify the sources of variability of the different growth components. The approach is complex, but provides important insights to the effect of the environment on growth and survival of individuals in nature, much more economically than other methods that involve extensive environmental and biological sampling (Campana and Jones 1992).

Applications in larval fish ecology have been extensive. IGH's reconstructed from larval and juvenile fish otolith growth increments have revealed critical ecological transitions (Brothers and McFarland 1981; Jenkins and Davis 1990) and compared growth conditions of different year-classes (Butler 1989; Thorrold and Williams 1989; Hovenkamp and Witte 1991; Moskness and Fossum 1992), spawning groups (Moskness and Fossum 1991), hatching dates (Penney and Evans 1985), nursery grounds (Karakiri et al. 1989; Moskness 1992; Burke et al. 1993) and seasons (Hovenkamp 1989; Koutsikopoulos et al. 1989). More sophisticated time-series analyses have evaluated the effects of temperature and other environmental variables on otolith daily growth (Gutierrez and Morales-Nin 1986; Maillet and Checkley 1991). Finally, size-selective

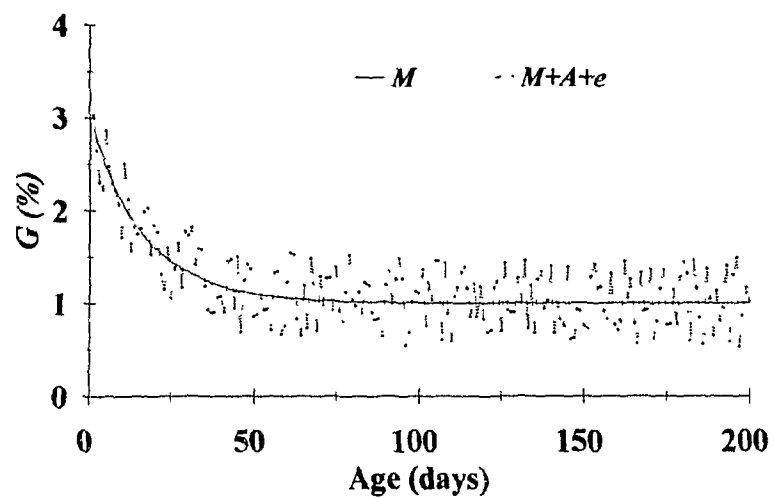


Figure 1.5. Schematic view of an individual specific growth rate (G) series reconstructed from gladius analysis. The unbroken line represents the mean growth component (M) usually related to the size effect. t , is the time interval corresponding to the deposition of one increment.

mortality during early life, has been detected and estimated historically from otolith-reconstructed length and growth-rate frequency -distributions (Neilson and Geen 1986; West and Larkin 1987; Post and Prankevicius 1987; Pepin 1989; Campana and Jones 1992; Hovemkamp 1992).

In squids, the approach is new. Statolith daily growth increments, widely used to estimate the age of squids, were used in a preliminary attempt to reconstruct the paralarval growth history of *Abralia trigonura* (Bigelow 1992). The suitability of these structures for growth reconstruction, however, appears to be limited, since the planes of calcium deposition in the statoliths may vary considerably throughout ontogeny (Arkhipkin 1991). Alternatively, the gladius structure correlates well with somatic growth and the interpretation of its accretive growth has been regarded as promising for IGH reconstruction (Bizikov 1991; Arkhipkin and Bizikov 1991; Arkhipkin and Perez in press). Another important advantage is the fact that gladii are not damaged by common fixatives, so that preserved material can be studied.

1.3. Objectives

The seasonal and geographic distribution of the early stages of *I. illecebrosus* was described from an intense parlarva and juvenile sampling program in the late 1970's and throughout the 1980's (Rowell et al. 1985; Dawe and Beck 1985a and b). The gladius technique provided an opportunity to reconstruct growth of juveniles collected in these surveys and to address ecological pressures acting on the early life phase during the collapse of the fishery. The analyses focused in two major sources of growth variability: (a) life history events including ontogenic transitions of life-styles and ecological niches; and (b) variations of the environment, mostly associated with gradients of temperature and food availability experienced during the early life. These gradients are established in terms of the oceanographic structure of the juvenile habitats (Gulf Stream / Slope Water frontal zone), latitudinal range of the species distribution, and seasonal and interannual fluctuations of the environment. The main objectives were:

- a.) to evaluate the impact of the diverse environmental conditions to which *Illex* are exposed, on inter- and intrapopulation growth variability during early life.
- b.) to assess whether juvenile growth reflects annual squid productivity and, therefore, it can be used as an indicator of recruitment success.
- c.) to assess whether historical collections of squid gladii could be used as an annual index of biological production in the shelf/slope system.

If, within a geographical population component, individual growth is relatively homogeneous and reflects annual survival conditions, it is hypothesized that a relationship could be established between the interannual variation of juvenile growth and the observed levels of squid abundance on the feeding grounds. Similarly, because squid are a highly mobile annual species, they may integrate overall annual production. One important limitation to these hypotheses derives from the environment-induced growth variability; if juvenile growth, within a population component, is heterogeneous and determined mostly by local or seasonal patchiness of the environment, its suitability to predict overall biological production and annual recruitment would be limited. These hypotheses were addressed on the winter population component of *I. illecebrosus* that recruits off Nova Scotia and involved the study of juvenile growth patterns and their environmental causes during the years of fishery collapse.

This study is divided in two main parts. The first part (chapter 2) consists of an evaluation of the suitability of the gladius structure for age determination and IGH reconstruction in *I. illecebrosus*. With the potentials and limitations of the technique defined, the remaining chapters apply gladius growth histories to address ecological processes affecting growth and survival during *Illex* early life. In chapter 3, gladius growth variation as a function of size is used: (a) to detect ecological shifts and sexual differentiation, and (b) to evaluate the overall effect of food and temperature gradients on size-specific growth. This effect is approached in depth in chapter 4, using gladius growth histories of juveniles collected across the Gulf Stream/ Slope Water frontal system, during five consecutive surveys. Physical transport and retention processes are also discussed. Finally, chapter 5 addresses the responses of individual growth to seasonal, interannual

and geographic variations of the environment. An attempt to establish a relationship between juvenile growth and annual recruitment is made.

Throughout this thesis the following terms are used to define early life history stages of *I. illecebrosus*:

Paralarva - Planktonic stage that follows hatching and ends with the appearance of functional tentacles and the onset of body elongation.

Juvenile - Macroplanktonic and micronektonic stages characterized by the elongation of the body and the appearance of subadult and adult morphological features.

Subadult - Fully nektonic stage that occupies the adult habitat but that is smaller and sexually immature.

Juvenile growth phase - The developmental period comprised between the paralarva - juvenile transition to the attainment of the adult life style.

Early life history - Set of events occurring during the paralarval and juvenile stages.

CHAPTER 2. Evaluation of Gladius Structure for Age and Growth Studies of the Short-Finned Squid, *Illex illecebrosus*.

2.1. Introduction

During the past 20 years, significant advances on cephalopod population biology have derived from the development of indirect methods of ageing (see Jereb et al. 1991 for review). Analogous to fish otoliths, cephalopod statoliths have been shown to provide reliable age estimates in days and have become the main tool for the study of growth, cohort analysis and life-history reconstruction (Caddy 1991; Jackson in press; Arkhipkin and Perez in press). More recently, the potential of another cephalopod skeletal structure, the gladius, for age and growth studies has been investigated (Bizikov 1991; Arkhipkin and Bizikov 1991; Jackson et al. 1993).

The gladius is the internal shell present in squids and some sepiolids. Already formed at the time of hatching, the gladius structure is uncalcified and mainly composed of the polysaccharide β -chitin in association with proteins (Hunt and Nixon 1981). Periodic growth marks were first observed by Naef (1922) and LaRoe (1971). Bizikov (1991) described the internal structure of the gladius and showed that, homologous to the shell of other mollusks, it was formed by a median shell layer (**ostracum**), an inner ventral shell layer (**hypostracum**) and an outer shell layer (**periostracum**), with different planes of accretive growth potentially suitable for age interpretation.

By comparison with statolith-determined age, preliminary studies have supported the daily deposition of the growth marks on the periostracum and the hypostracum of the squids *Kondakovia longimana* and *Berryteuthis magister* respectively, suggesting that such growth layers are suitable for age and growth studies (Arkhipkin and Bizikov 1991, Bizikov 1991). In ommastrephids and loliginids, ostracum growth increments have been found to be deposited with a near daily periodicity, but the total age determination on this layer could not be obtained. Responsible for the gladius longitudinal growth, however, the ostracum parallels the growth of the mantle length and may provide accurate size-specific

growth rate estimates (Arkhipkin and Bizikov 1991, Bizikov 1991, Jackson et al. 1993, Bizikov in press). Since mantle length is the standard measure of squid size (Amaratunga and Durward 1978; Roper and Voss 1983) applications are direct and wide-spread. Size-specific growth has been shown to provide important insights in the growth performances of both groups and individuals, thus complementing applications of age based on statolith on squid population ecology (Arkhipkin and Perez in press).

This chapter investigates the accretive growth of the gladius of *I. illecebrosus* and evaluates its potential for age determination and reconstruction of growth histories. The analysis will estimate the sensitivity and limitations of the gladius technique that will be applied, in the subsequent chapters, to address ecological processes affecting growth during *Illex* early life.

2.2. Material and Methods

Frozen samples of the short-finned squid (*Illex illecebrosus*) obtained from the commercial fishery and from one research cruise of the R/V "Petrel", were collected by bottom trawls on the Scotian Shelf, off Nova Scotia, Canada, during the summer of 1991. Juvenile squid, preserved in 75% ethanol, were caught by midwater trawls during eight research cruises conducted between the Gulf Stream and the shelf/slope front from 1979 to 1989 (Appendix 1). One *Illex* paralarva, was obtained from a plankton survey in January 1986 and was preserved in formalin (4%). Frozen squid were thawed, weighed (W), the dorsal mantle length (ML) measured, and both statoliths and gladii were extracted and stored in ethanol (75%) and formalin (10%) respectively. Only the gladius was extracted from the preserved squid. After the measurements were taken on preserved specimens, the mantle was briefly plunged into a solution of NaOH (1N) at approximately 60°C to soften the mantle tissues and facilitate gladius extraction.

2.2.1. Gladius analysis

The paralarval gladius was examined under a Nanolab 2000 Scanning Electron

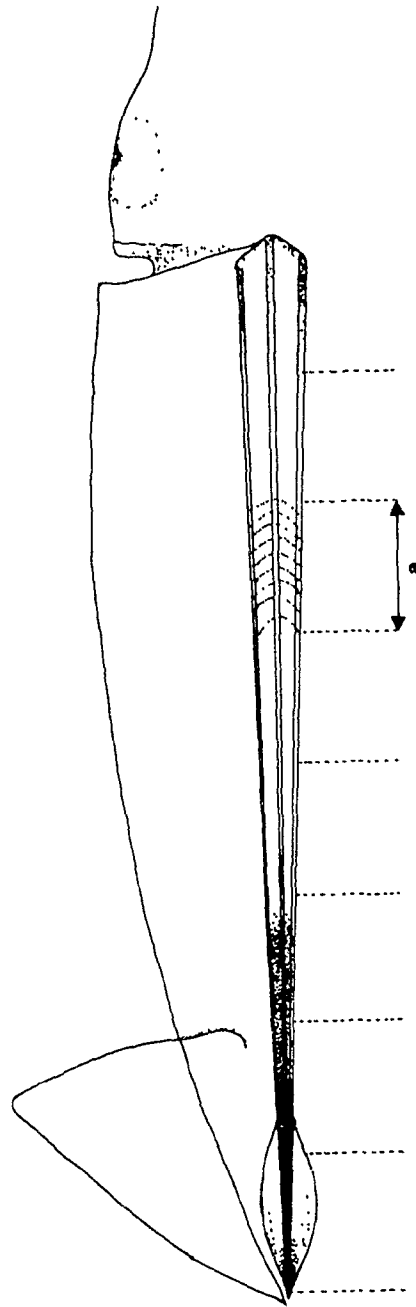


Figure 2.1. Schematic dorsal view of *Illex illecebrosus* gladius and position in relation to the squid mantle. **a**, represents one centimetre interval. The neck of the gladius (shaded area) corresponds to the portion of the gladius where the growth marks are not distinguished.

Microscope. The gladius was mounted on an aluminum stub with double-sided tape, air dried for 24 hours, and coated in a vacuum evaporator with 82 Å of gold. In juveniles and adults, the gladii were prepared and initially read using the 'relative growth' technique, for comparison with the results of Bizikov (1991). Each gladius was measured for total length (GL) and marked at ten millimetre intervals from the posterior (fins) to the anterior end (head) (Fig. 2.1). The dorsal surface of the gladius plate (ostracum growth layer) was then examined under a Zeiss dissecting scope at low magnification (20 to 30X) using a combination of incident and transmitted light to optimize the visualization of growth marks. Growth marks of the ostracum growth layer were counted per gladius length interval from the anterior (head) towards the posterior (fins) end until the marks were no longer visible (Fig. 2.1). The mean spacing between growth marks (mean growth increment in mm) was calculated by dividing 10 mm by the number of growth marks counted in each gladius length interval. More detailed analyses of growth rate were also performed (see below).

The precision of gladius mark counts was assessed by comparing three blind counts of thirty selected squids made independently by a single reader with a one month interval between counts. The total number of marks counted in a fixed proportion of the gladius length on the three occasions were compared by: (a) the Average Percent Error (APE; Beamish and Fournier 1981), which calculates the average percentile deviation of each count from the mean value obtained for the three counts; and (b) the Coefficient of Variation (CV; Chang 1982), which expresses the standard deviation of the three counts as a percentage of the mean.

Gladius growth histories were also reconstructed in preserved specimens that were kept in the 15 m diameter pool of the Aquatron Laboratory of Dalhousie University in 1978 for tagging, feeding and growth experiments (O'Dor et al. 1980). Gladii were extracted from three preserved specimens identified by their colour-coded tags: male tag red-yellow-orange (**RYO**), 170 mm ML, 118 g W; male tag red-green-red (**RGR**), 195 mm ML, 148 g W; and female tag red-orange-red (**ROR**), 235 mm ML, 246 g W. The squids were captured and tagged on 18 July, 1978 and feeding was individually controlled between 19 July and 4 August. After that the individuals were allowed to feed freely

(O'Dor et al. 1980). RYO, RGR and ROR survived 24, 18 and 56 days in the tank respectively. Series of growth increments (GInc) were obtained by displaying the image of the gladius dorsal surface on a monitor screen and measuring distances between consecutive growth marks with an Image Analysis System (Bioscan® - OPTIMAS). Each growth series was qualitatively compared to monitored feeding rates and temperature fluctuations. In the female ROR, which survived longer than the other two and experienced significant temperature variations in the tank, a technique of multiple series analysis known as transfer function (Box and Jenkins 1976) was employed to represent the magnitude and lag of growth variability (dependent series) in response to temperature fluctuations (independent series). In the analysis, the temperature series was "differenced" in order to remove the increasing trend (Box and Jenkins 1976).

2.2.2. Statolith analysis

In order to investigate the rate of deposition of gladius increments, statolith daily increments of 20 selected squids were compared to counts of their gladius growth marks. Age was determined on the statolith structure according with the method described in Dawe et al. (1985) and reviewed in Jereb et al. (1991). The right statolith of each squid was mounted on a glass slide and ground in the sagittal plane. Statolith ground surfaces were examined under a light microscope at 200x magnification with a camera lucida, and a drawing pen was used to outline the projected growth increments on a paper pad. The total number of growth rings, counted along the axis of maximum growth, was compared to the number of growth increments deposited anterior to 100 mm of the gladius length of the same individuals (Fig. 2.1).

2.3. Results

2.3.1. Relationship between gladius and somatic growth

Gladius length was measured in 1576 squids including preserved and fresh-frozen

Table 2.1. Linear regression of gladius length (GL) on mantle length (ML), and of the Log GL on Log weight (W) of specimens **preserved, fresh-frozen** and fresh-frozen **corrected** for preservation. *n*, number of regression points; *a*, intercept; *b*, slope; c.i., confidence interval at $\alpha=0.05$, r^2 , coefficient of determination. The asterisks indicate that the slopes calculated for preserved specimens were found to be significantly different ($p<0.05$) from the slopes calculated for fresh-frozen specimens even after correction for the fixative effect.

ML x GL					
	<i>n</i>	ML range	<i>a</i> \pm c.i.	<i>b</i> \pm c.i.	r^2
Preserved	1393	7.8-92.3	5.235 ± 0.273	1.027 ± 0.008	0.977
Fresh-frozen	183	118-201	13.881 ± 4.759	$0.874 \pm 0.031^*$	0.946
Corrected	183	118-201	15.458 ± 4.678	$0.905 \pm 0.031^*$	0.946
Total	1576	7.8-201.0	8.178 ± 0.208	0.920 ± 0.004	0.994
LogW x LogGL					
	<i>n</i>	W range	Log <i>a</i> \pm c.i.	<i>b</i> \pm c.i.	r^2
Preserved	1393	0.04-16.11	1.593 ± 0.002	0.355 ± 0.004	0.972
Fresh-frozen	154	30.0-151.0	1.648 ± 0.026	$0.295 \pm 0.014^*$	0.916
Corrected	154	30.0-151.0	1.565 ± 0.026	$0.297 \pm 0.014^*$	0.916
Total	1547	0.04-151.0	1.587 ± 0.002	0.339 ± 0.002	0.986

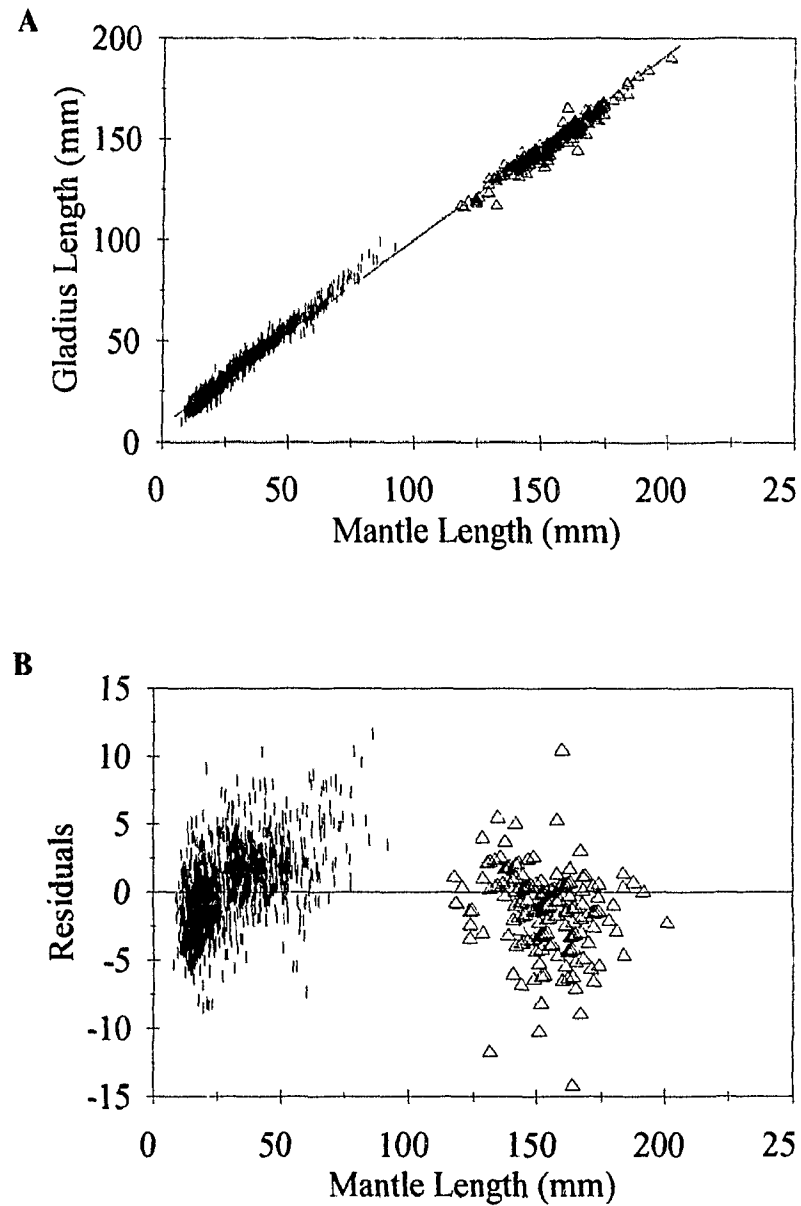


Figure 2.2. Relationship between Mantle Length and Gladius Length. (A) Linear regression, $GL = 8.13 + 0.92ML$ ($r^2 = 0.994$) and (B) residuals. Vertical bars represent preserved specimens; triangles represent fresh-frozen specimens.

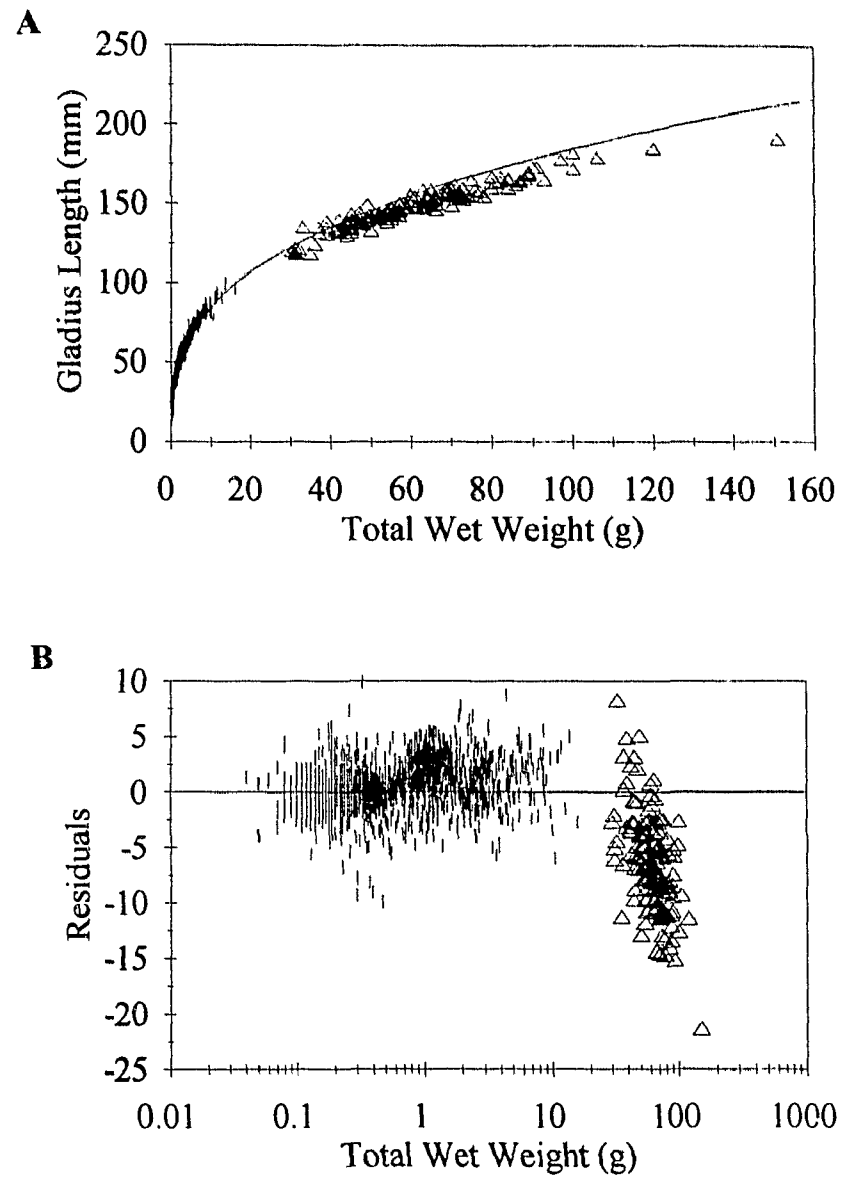


Figure 2.3. Relationship between total wet weight and gladius length. (A) Model fitted after log linearization of the variables, $GL = 38.64ML^{0.339}$ ($r^2 = 0.986$); and (B) residuals. Vertical bars represent preserved specimens; triangles represent fresh-frozen specimens.

individuals (Table 2.1). A strong linear correlation was found between ML and GL (Fig. 2.2A) with ML explaining 99.4% of the total variance of GL (Table 2.1). A curvilinear model was fitted to the relationship between GL and total wet weight ($r^2=0.986$) after the log-linearization of the variables (Fig. 2.3A; Table 2.1).

The residual analysis of both relationships, however, showed that GL of large/fresh-frozen squids were usually underestimated by both fitted models (Fig. 2.2B and 2.3B). When compared, slopes of regressions calculated separately for preserved and fresh-frozen squids were found to be significantly different (Table 2.1), indicating a preservation artefact in the relationship between GL and somatic growth. This artefact derives mostly from the dehydration of the mantle in ethanol which causes both the shrinkage of the tissues and the loss of weight.

An additional 19 fresh squid were weighed and had their mantle length measured before and after fixation in formalin and preservation in ethanol (75%) for 40 days. A linear relationship obtained between preserved and fresh ML ($r^2=0.866$) and W ($r^2=0.983$) provided a factor that was then used to correct the ML and the W of the fresh frozen squids used in the relationships between GL and somatic growth. After correction, however, the slopes were still significantly different ($p<0.05$; Table 2.1).

2.3.2. Gladius morphology and growth increments

In *Illex illecebrosus*, the gladius is typical of a pelagic, fast-swimming, open-ocean squid. It consists of a narrow central **rachis** with two lateral ribs and a terminal spoon-shaped **conus** (Fig. 2.1). The longitudinal growth of the gladius plate occurs by the deposition of chitin layers to the ventral surface from the fins towards the head (Fig. 2.1 and 2.4A). During periods of low growth, such layers crowd together and form a distinct discontinuous mark that resembles the anterior border of the gladius (Fig. 2.4B); the marks closer to the anterior border being the ones that delimit the increments more recently deposited.

In juveniles and adults, growth marks are observed on the dorsal surface of the rachis (Fig. 2.4B). These marks become faint as the gladius plate narrows posteriorly and

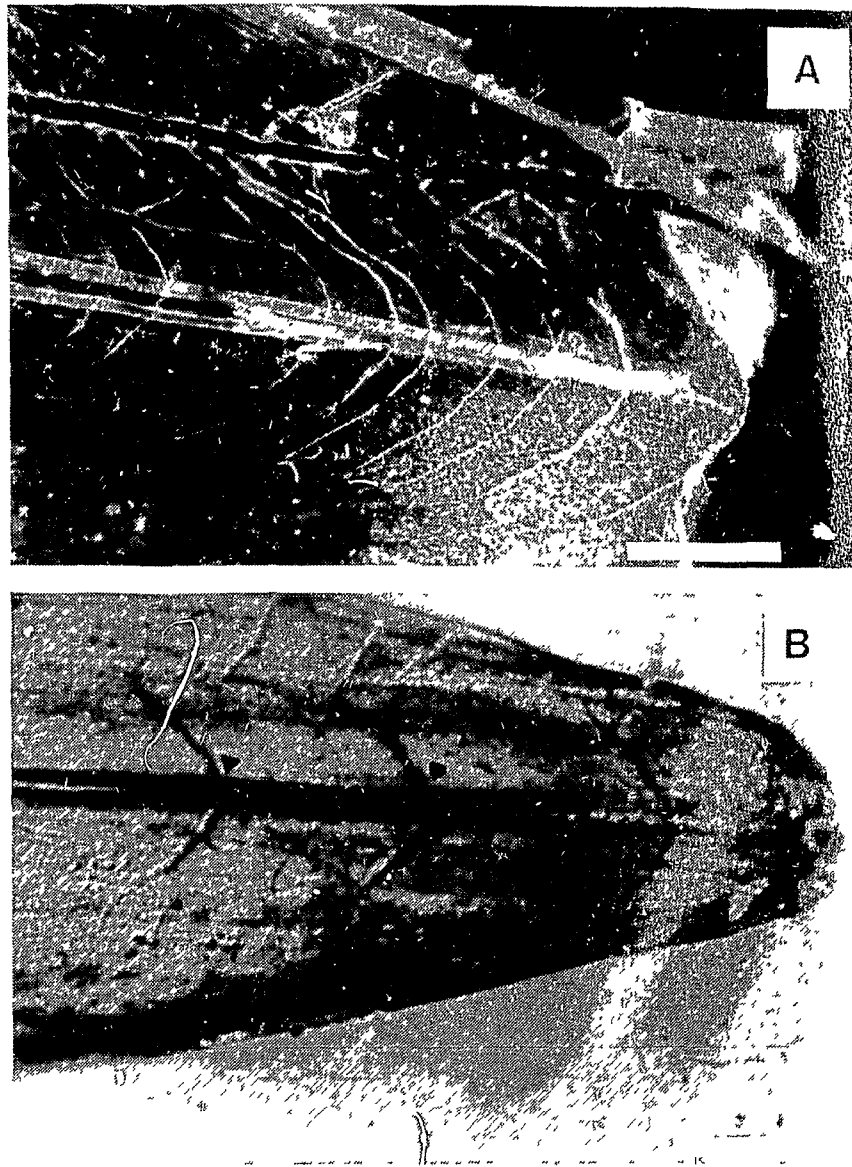


Figure 2.4. Accretive growth of the ostracum layer on the gladius of *Illex illecebrosus*. (A) Deposition of layers near the anterior border (head), horizontal bar=0.1 mm; (B) Growth marks as observed on the dorsal surface of the gladius plate (triangles), horizontal bar= 0.5 mm.

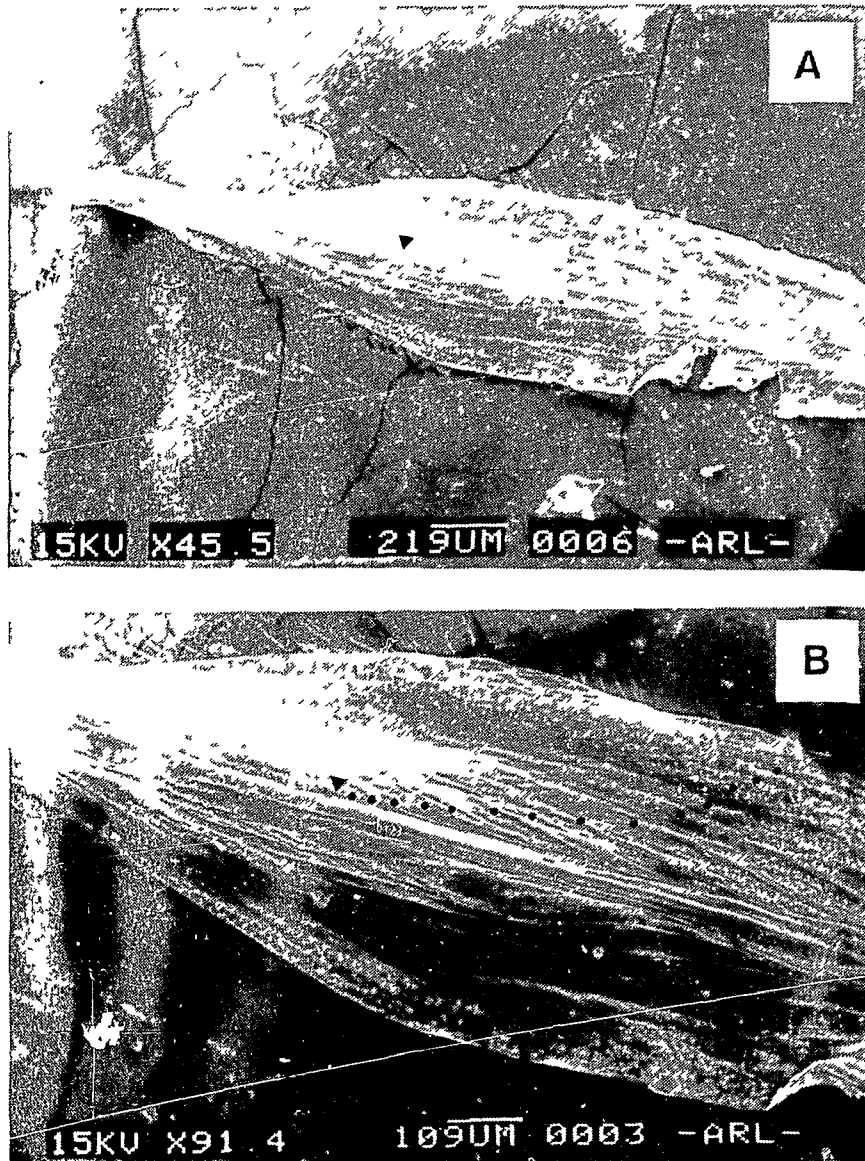


Figure 2.5. Scanning Electron Micrographs of the dorsal gladius structure of an *Illex illecebrosus* paralarva (3.7 mm GL) (A) 45.5x magnification; (B) 91.4x magnification. Triangles indicate estimated GL at hatching. The anterior end of the gladius is to the right side

cannot be distinguished in the neck and the conus region (Fig. 2.1). Because the early gladius growth is masked, the absolute number of growth increments on the ostracum shell layer could not be determined.

In the paralarva, regularly spaced growth marks appeared as ridges on the dorsal surface of the broad and relatively longer conus (Fig. 2.5). The first growth mark, probably corresponding to the hatchling gladius, was not readily distinguishable (Fig. 2.5B). From estimations of GL at hatching, however, it is possible that the total number of growth marks counted anterior to this length corresponds to the absolute age. *I. illecebrosus* hatched in the laboratory measured around 1.1-1.25 mm ML (O'Dor et al. 1986). In Figure 2.5B, about 14 marks can be counted between 1.1 mm GL and the anterior border of the conus.

2.3.3. Growth Increment interpretation

Gladius growth was analyzed in 343 squids ranging from 11 to 201 mm ML and 0.2 to 151 g W. On average, growth marks were visible in the anterior half of gladius plate (mean % readable of GL = 49.12 ± 9.75), but were altogether unreadable in 18 gladii. The number of marks counted per centimetre interval of gladius length ranged from 7 to 26. The mean spacing between growth marks within a gladius length interval, was more variable and increased from 0.55 to 0.76 mm on average in the earliest deposited 20 to 50 mm of the gladius length (Table 2.2). In gladii longer than 60 mm, increment variability decreased and the mean spacing stabilized at around 0.91-0.98 mm (Table 2.2).

The analysis of precision of growth increment counts in a fixed proportion of gladius length is shown in Table 2.3. Each of the three blind determinations deviated from the mean value obtained in the three counts, on average, by 3.77%. Furthermore, the standard deviation of the three counts represented, on average, 5.11% of the mean number of growth marks (Table 2.3).

The rate of increment deposition on the gladius plate was assessed by the relationship between the number of statolith and gladius growth increments of 20 selected

Table 2.2. Number of growth marks and mean increment width in millimetres (10 mm/ number of growth marks) per 10 mm of gladius length intervals. SD, standard deviation; *n*, number of GL intervals.

GL	<i>n</i>	Growth Marks			Incr. Width
		Mean	SD	Range	min-mean-max
0-10	-	-	-	-	-
10-20	45	18.14	1.91	15-20	0.38-0.55-0.83
20-30	53	15.85	1.64	12-20	0.50-0.63-0.83
30-40	44	14.28	1.74	11-18	0.55-0.70-0.91
40-50	37	13.06	1.85	11-17	0.59-0.76-1.00
50-60	26	11.30	0.93	10-14	0.71-0.88-1.11
60-70	78	10.26	0.95	8-13	0.77-0.97-1.25
70-80	122	10.35	1.12	8-13	0.77-0.97-1.25
80-90	158	10.43	1.06	8-13	0.77-0.96-1.25
90-100	178	10.47	1.17	7-14	0.71-0.95-1.43
100-110	181	10.62	1.22	7-14	0.71-0.94-1.43
110-120	179	10.57	1.13	8-14	0.71-0.95-1.25
120-130	173	10.69	1.22	8-14	0.71-0.94-1.25
130-140	139	10.55	1.26	8-14	0.71-0.95-1.25
140-150	85	10.58	1.35	8-14	0.71-0.95-1.25
160-170	38	10.29	1.21	8-13	0.77-0.97-1.25
170-180	11	10.45	0.78	9-12	0.83-0.96-1.11
180-190	5	11.00	0.63	10-12	0.93-0.91-1.00
190-200	1	10.00	0.00	-	--
Total	1553			7-26	

Table 2.3. Total number of growth marks counted on a fixed proportion of the gladius length of 30 squids in three consecutive occasions by the same reader with a one month interval between them. APE, average percent error; CV, coefficient of variability.

squid	Counts			Mean	APE	CV
	1	2	3			
281	63	53	62	59.33	7.12	9.28
282	94	84	86	88.00	4.55	6.01
283	96	74	81	83.67	9.83	13.43
284	82	72	73	75.67	5.58	7.28
285	98	79	84	87.00	8.43	11.32
291	73	66	71	70.00	3.81	5.15
292	78	77	86	80.33	4.70	6.14
293	78	75	81	78.00	2.56	3.85
294	75	71	78	74.67	3.27	4.70
295	74	67	78	73.00	5.48	7.63
296	82	81	80	81.00	0.82	1.23
297	73	70	74	72.33	2.15	2.88
298	71	70	78	73.00	4.57	5.97
299	63	61	64	62.67	1.77	2.44
300	61	60	64	61.67	2.52	3.38
303	87	80	84	83.67	2.92	4.20
318	75	72	68	71.67	3.41	4.90
320	75	70	75	73.33	3.03	3.94
332	93	81	84	86.00	5.43	7.26
336	71	70	78	73.00	4.57	5.97
338	76	73	74	74.33	1.49	2.05
339	92	91	90	91.00	0.73	1.10
340	89	87	87	87.67	1.01	1.32
342	95	89	87	90.33	3.44	4.61
343	64	59	62	61.67	2.88	4.08
344	62	67	66	65.00	3.08	4.07
356	96	93	95	94.67	1.17	1.61
135	72	67	62	67.00	4.98	7.46
273	88	76	75	79.67	6.97	9.08
275	61	60	61	60.67	0.73	0.95
mean				76.00	3.77	5.11

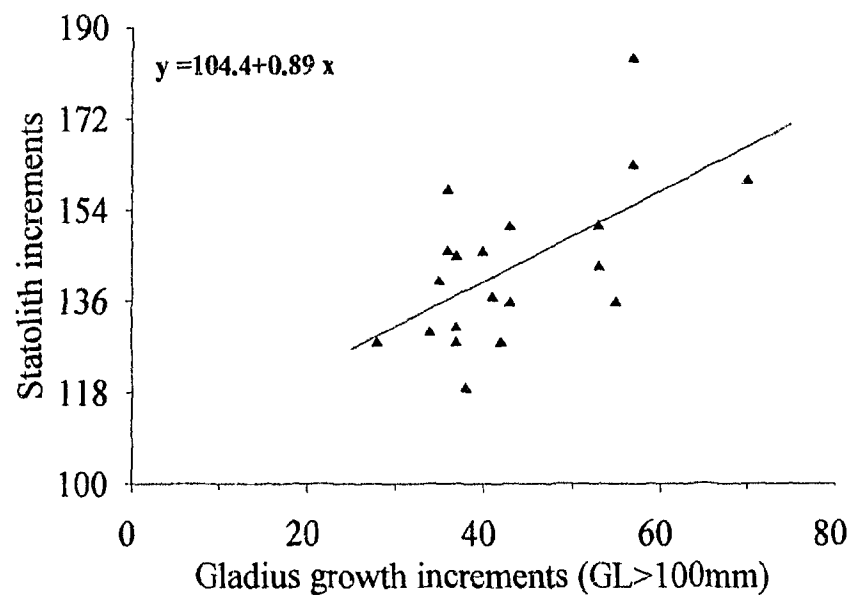


Figure 2.6. Relationship between the number of statolith growth increments and the number of gladius growth increments anterior to 100 mm GL. The solid line represents the linear model fitted to the data set ($r^2=0.37$).

squids (131 - 180 mm ML; 42 - 91 g W). A linear relationship with a slope of 1 would be expected if gladius growth increments were deposited at the same rate as the statolith increments. In addition, because gladius counts in each squid included all increments deposited anterior to 100 mm GL, this assumption predicts that the fitted line should intercept the y axis at an age estimate for 100 mm GL squid. Statolith and gladius growth increments correlated weakly ($r^2=0.366$). The slope obtained however (0.89 ± 0.21 c.i.) was not significantly different from the hypothesized slope 1 ($t=0.414$, $p>0.5$; Fig. 2.6), and a total of 104.4 statolith increments (± 25.9 95% c.i.) was estimated by the model for 100 mm GL. The number of statolith increments estimated for *Illex* spp. of 100 mm ML reported by other studies, vary between 115 and 120 (Hurley and Beck 1979; Morris and Aldrich 1985; Arkhipkin 1990).

2.3.4. Reconstruction of mean growth trajectory

A gladius growth curve was reconstructed from the cumulative number of growth marks counted in each centimetre of gladius length interval (Fig. 2.7). Assuming a daily deposition of growth marks, the curve was adjusted to the initial ages of 30, 40 and 60 days for the first 10 mm GL (not observed directly on the gladius surface) according to previous statolith age determinations for *I. illecebrosus* (Hurley and Beck 1979; Morris and Aldrich 1985; Balch et al. 1988). Gladius growth was found to be nearly linear after approximately 120 days (Fig. 2.7B).

2.3.5. Reconstruction of Gladius Growth Histories

Individual growth histories of the three captive squids are shown in Fig. 2.8 in relation to the temperature fluctuations and the feeding events during the monitored period. The male RYO had its stomach full at the time of tagging and had a 26 g meal the next day. The animal was not seen feeding for the next six days and had, after this period, five consecutive meals (ranging from 4.5 to 24 g) in the following five days. RYO lived for another 11 days on uncontrolled feeding. The gladius growth series shows peaks

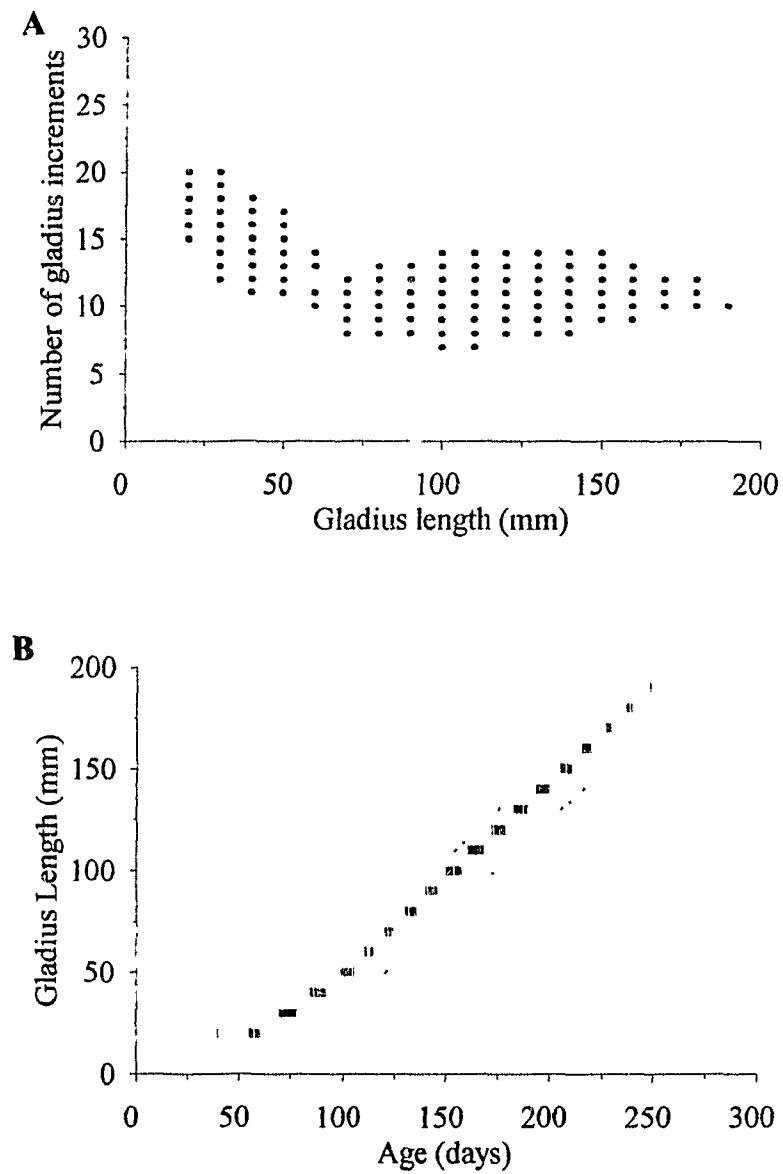


Figure 2.7. Growth curves reconstructed from gladius analysis. A, number of growth increments counted in 10 mm gladius length intervals. B, Cumulative number of growth increments at ages estimated with the following assumptions: statolith age estimations for the initial 10 mm GL were 40 days (vertical bars), 60 days (upper dotted line), 30 days (lower dotted line).

Figure 2.8. Reconstructed individual gladius growth history (increment width in mm) of three captive squids. A., Squid RYO, male, 170 mm ML; B., Squid RGR, male, 195 mm ML; C., Squid ROR, female, 235 mm ML. D., Temperature (°C) fluctuation at the bottom of the tank. Increment width series (dotted line) were smoothed (solid line) after the application of a statistical filter (see chapter 3). Solid vertical bar represent feeding rates (in g) in the tank during the controlled period from 10 July to 4 August, 1978 (horizontal bar).

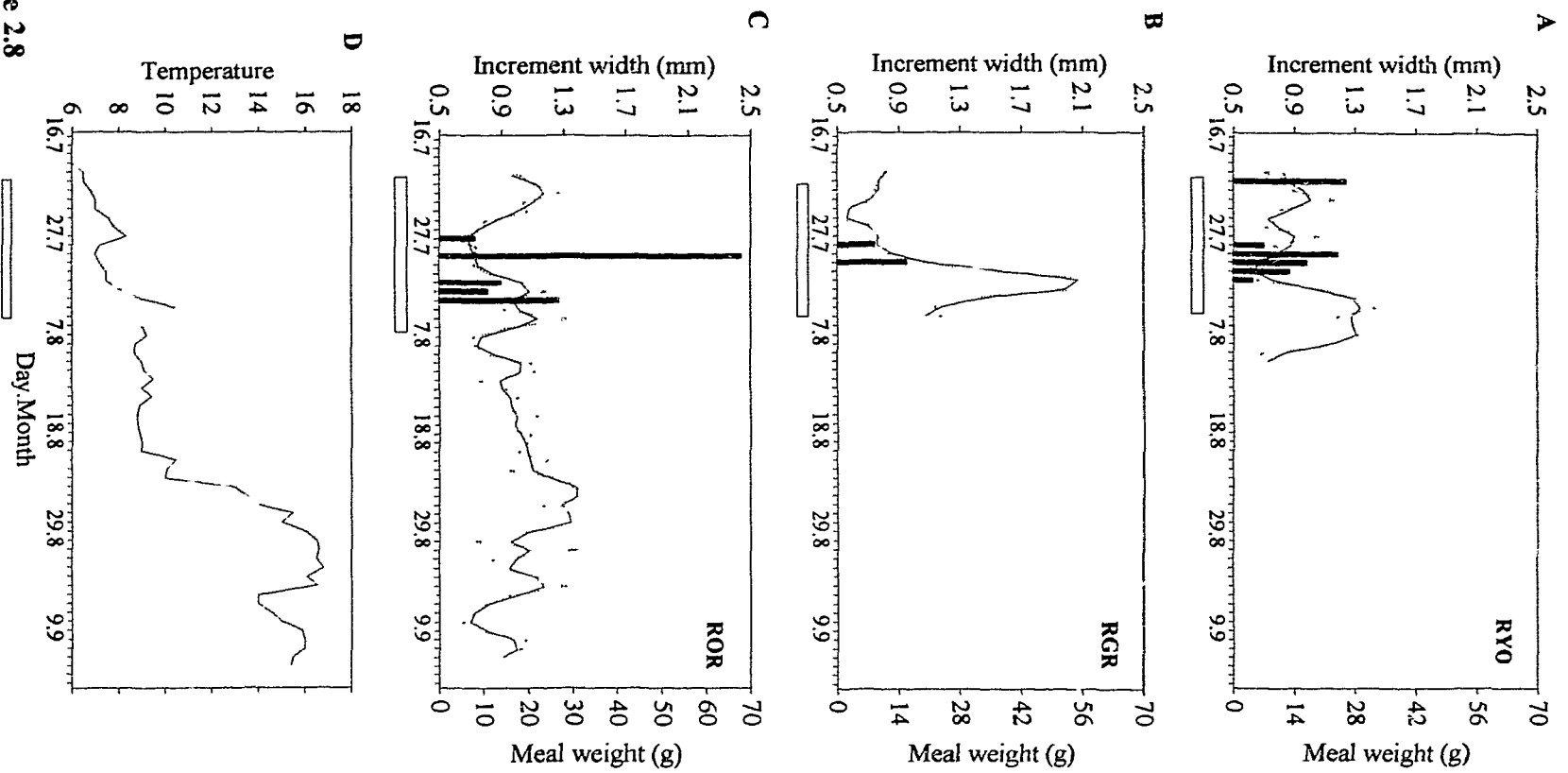


Figure 2.8

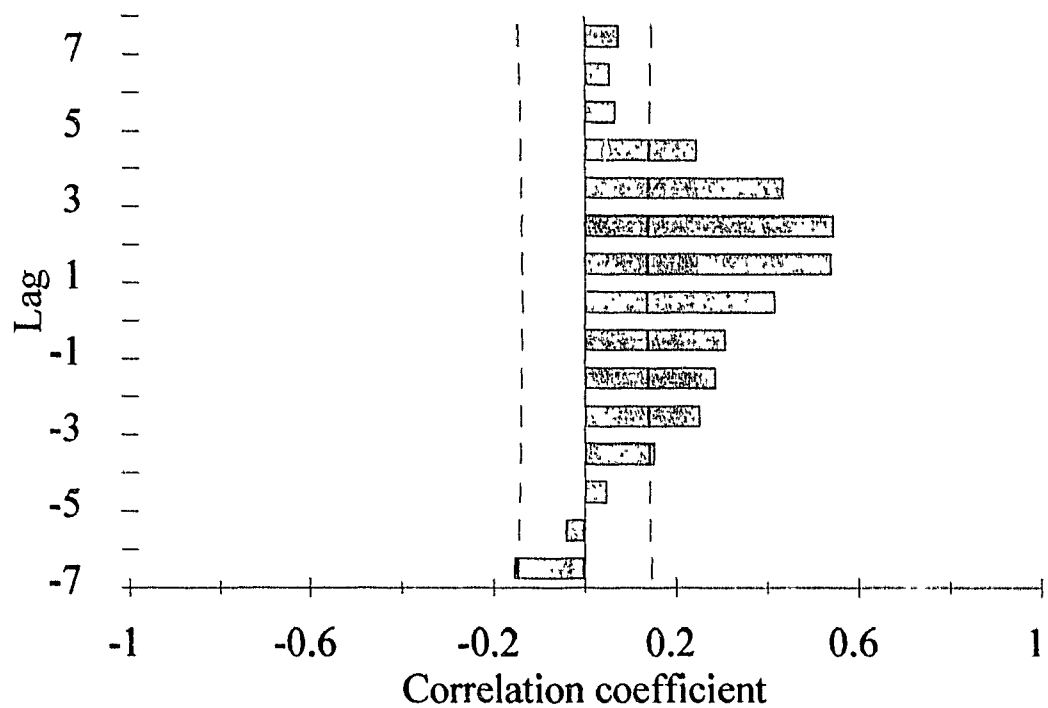


Figure 2.9. Pattern of estimated cross-correlation between the water temperature differenced series moved over the gladius growth series of the female ROR. The broken lines represent the standard error. Higher positive correlations occur at 2 and 3 day lags.

in growth increment succeeding both feeding episodes observed (Fig. 2.8A). The male RGR did not eat until nine days after being brought to the tank. In the following three days it had 2 meals (8.5 and 16 g) and was fed freely for another 7 days until it died. The growth increments increased sharply after the meals and remained high for another four days during the uncontrolled feeding period (Fig. 2.8B). The female ROR fed for the first time eight days after capture. Five meals (ranging from 8 to 68g) were taken in the eight following days. ROR lived for another 43 days on uncontrolled feeding and was found to be in advanced maturity stage at death. An increase in growth rate followed the feeding periods (Fig. 2.8C), especially after the second meal which was the largest observed during the whole experiment (R. K. O'Dor, pers. com.). This animal experienced a water temperature increase after the feeding experiments (Fig 2.8D). The temperature series cross-correlated with the growth increment series indicated a significant positive response of growth lagging the temperature variation by 2 - 3 days (Fig. 2.9). A general decrease in growth rate during the last three weeks, despite sustained high temperatures, was probably related to the fact that the animal was reaching sexual maturity and investing more growth in gametes (Fig.2.8C-D).

2.4. Discussion

The age of an organism can be interpreted from the accretive growth of a skeletal structure provided that: (a) the periodicity of increment deposition is known; and (b) the structure's time record includes all the animal's life time. Furthermore, if the deposition rate of skeletal material is proportional to somatic growth, growth increments on the structure can be used to back-calculate somatic growth at previous occasions (Campana and Neilson 1985). There are three previous evaluations of the gladius plate structure (ostracum growth layer) for age determination and growth studies in the ommastrephid squids *Illex argentinus* and *Sthenoteuthis oualaniensis* and the loliginid *Sepioteuthis lessoniana* (Bizikov 1991; Arkhipkin and Bizikov 1991; Jackson et al. 1993). All of them concluded that: (a) the gladius plate is likely unsuitable for age determination; (b) the gladius increments are linearly related with the mantle growth and may provide accurate

estimates of individual size-specific growth rates; and (c) at least during the adult stage, the deposition of gladius increments approximates daily periodicity. These same conclusions and further distinctions were evident in the present results on the gladius plate structure of the short-finned squid, *Illex illecebrosus*.

The early growth of the gladius plate is progressively masked by structural modification as growth layers are continuously added to the ventral surface. Consequently, only a fraction of the growth increments can be enumerated in older animals and the total age cannot be estimated. This posterior faint zone may already be present in paralarval gladius since the total number of visible marks in the single paralarval gladius examined, was found to be nearly half of statolith daily rings counted in similar sized paralarvae (Balch et al. 1988). Further investigation, however, is needed because 14 days is not an unrealistic age for a 3.8 mm GL squid.

The gladius plate increment deposition was proportional to the lengthening of the mantle throughout juvenile and adult life. The relationship, however, is altered by the shrinkage of the mantle in preserved specimens. The gladius lies free in the shell sac along the dorsal midline of the mantle and is highly flexible. As the mantle shrinks the gladius tends to bow, the result being that it is longer than the projected mantle length (usually measured in most cephalopod studies). Although this effect can be reduced by using preserved/fresh mantle length correction factors, it is best to avoid mixing individuals preserved or handled differently when gladius increments are to be transformed into mantle growth rates. In general, because gladius growth correlates strongly with somatic growth and its length is less variable than the mantle length, gladius length may be the best linear measurement of size (Kristensen 1983) and gladius growth increments excellent indicators of size-specific somatic growth (Bizikov 1991; Arkhipkin and Bizikov 1991; Jackson et al. 1993; Bizikov in press).

The enumeration of gladius growth marks was consistent in this study and, at least during the adult phase, growth increments seem to approximate daily mantle growth rates estimated independently. Mean growth increments along the gladius plate were similar to values obtained for *I. argentinus* (0.9 - 2.0 mm, GL range between 150 and 300 mm) and for *S. oualaniensis* (0.77, 0.79, 1.25 mm, averages between 30 and 270 mm GL for males,

medium-sized and large females respectively; Bizikov 1991; Bizikov in press). Furthermore *I. illecebrosus* gladius increments fell within the ranges of mean daily size-specific growth rates estimated from statolith analysis and ML frequency distributions (Table 2.4). Mean gladius growth rates inferred here were lower than statolith-determined rates for the Scotian Shelf (Arkhipkin 1990; Morris and Aldrich 1985) and higher than rates obtained for inshore Newfoundland (Dawe and Beck 1992), although minimum and maximum gladius increments overlapped those levels. Similar results were obtained in comparison with estimates for *I. argentinus* (Table 2.4). Mean growth increments estimated for gladii under 100 mm were less consistent and seem to overestimate directly measured growth increments (see results of Chapter 3). This indicates that the estimation of gladius size-specific growth rates by Bizikov's (1991) 'relative growth' method may not be accurate for juvenile squid gladius.

The growth reconstructed from gladius analysis covered nearly two thirds of the life of *Illex*. The paralarval phase (GL<10 mm) and mature stages (GL between 200 and approximately 300 mm GL) were not included. A predominantly linear trajectory of GL was preceded by slower juvenile growth in accordance with curves reconstructed for other species from gladius growth (Bizikov in press; Bizikov 1991; Arkhipkin and Bizikov 1991). In the ommastrephid *S. oualaniensis*, when large mature squids were included, an S-shaped growth curve was obtained because of an additional phase of growth decline at the end of life (Bizikov in press). The difficulties in fitting of growth models to size-at-age plots largely derive from individual growth variability (Jackson in press). Because growth trajectories of individuals may vary considerably depending on variable environmental conditions, size-at-age plots of individuals sampled in different seasons or areas exhibit large variation. Size-specific growth of gladii measured on individual squid, should provide more accurate descriptions for general growth models of squid.

At the individual level, it is suggested that the variation of growth increments in the gladius plate may be sensitive to feeding events, temperature fluctuations and possibly sexual maturation. The complete digestion of a large meal of live fish by *I. illecebrosus* may require over 30 hours at temperatures around 10°C (Wallace et al. 1981). Thus

Table 2.4. Daily size-specific growth rates (mm/d) reported in the literature, and calculated by statolith size-at-age analysis (s) and modal displacement of ML frequency distributions (m). References: (1) Arkhipkin (1990); (2) Dawe and Beck (1992); (3) Morris and Aldrich (1985); (4) Squires (1967); (5) Mesnil (1977); (6) Arkhipkin and Scherbich (1991); (7) Arkhipkin and Laptikovskiy (in press). ¹, females; ², males. Growth rates estimated in this study are indicated in bold for comparison.

Species	ML range (mm)	Growth rate (mm/d)	Reference
<i>I. illecebrosus</i>	10-190	0.38-1.43	
	30-110	1.26-1.43	1 (s)
	110-235	1.33-1.43	
	117-245	0.88 ¹	2(s)
	116-215	0.66 ²	
	33-266	1.78	3 (s)
	>140	0.33-1.33 ¹	4 (m)
		0.66-1.00 ²	
	8-120	0.66 ¹	5(m)
	8-115	0.58 ²	
	143-220	0.67 ¹	
	141-211	0.60 ²	
<i>I. argentinus</i>	<50	0.36-0.93	1,6,7 (s)
	50-100	0.73-1.67	
	100-200	0.83-1.73	

growth responses lagging 3 to 5 days after feeding events, as suggested by the present results, do not seem unreasonable. Temperature directly affects metabolic and feeding rates (O'Dor and Wells 1987) and may cause a more immediate response in growth such as shown by the ROR female. Although the limited material available and the difficulty of reproducing such experiments with ommastrephid squids prevented further conclusions, gladius structure seems to have good potential as a tool for reconstructing individual growth histories and assessing internal and external factors affecting growth. Further experiments of this sort, on more tractable loliginids, are desirable. Preliminary attempts to reconstruct individual growth histories of *I. illecebrosus* on the Scotian Shelf have related growth patterns with food encounters and have revealed different growth performances of schools and sex groups (Perez and O'Dor in prep.). Lunar cycles and maturation process were additional factors detected in the variability of growth rates of female *S. oualaniensis* in the Arabian Sea (Bizikov in press). The method appears to be promising for detecting growth variation in juvenile *I. illecebrosus* and assessing its environmental causes.

Finally the results indicate that, during the adult life, gladius increments and statolith rings are deposited with the same periodicity. A similar analysis, for *S. lessoniana*, concluded that such proportionality was restricted to the adult life (Jackson et al. 1993). For *I. argentinus* and *S. oualaniensis* daily periodicity was suggested based on the similarity between growth trajectories estimated by both gladius and statolith analysis (Arkhipkin and Bizikov 1991; Bizikov 1991). Our direct comparison with statolith-determined age included a relatively small number of individuals of a limited size-range, and showed considerable scatter in the data. Conclusions about the daily deposition of gladius increments, should be therefore considered with caution. Combined with the evidence provided by the size-specific growth and the individual growth histories reconstructed for captive squid, however, the daily nature of gladius increments is supported. Additional direct validation (Natsukari et al. 1991) would still be useful.

CHAPTER 3. Critical Transitions in Early Growth Histories of *Illex illecebrosus* Reconstructed from Gladius Analysis

3.1. Introduction

Patterns of early life history in cephalopods range from (a) direct development with the assumption of the adult niche immediately after hatching, to (b) nearly indirect development with the existence of ontogenetic stages that occupy distinct ecological niches (Boletzky 1974; Boletzky 1987; Vecchione 1987; Young and Harman 1988). *Illex* spp., and other ommastrephid squids, have been associated with the latter extreme of this range exhibiting a distinct planktonic phase (rhynchoteuthion stage) and at least one major morphological transition, although others have also been suggested (Vecchione 1979; Roper and Lu 1979; Nesis 1979b; Brunetti 1990; Vidal 1994a). The early life stage has been regarded as highly vulnerable and critical for pre-spawning survival (Vecchione 1987).

Our knowledge of the early life history of *Illex illecebrosus* derives from observations of paralarvae hatched in captivity (O'Dor et al. 1986), studies of the post-embryonic development (Roper and Lu 1979; Vecchione 1979; Nesis 1979b) and considerable data on the seasonal, spatial and vertical distribution of early life stages in the northwest Atlantic (Fedulov and Froerman 1980; Froerman et al. 1981; Amaratunga 1981; Dawe et al. 1982; Dawe and Beck 1985a and b; Rowell et al. 1985a; Hatanaka et al. 1985b and others). Embryonic development and hatching presumably occur within the warm waters of the Gulf Stream; the early life is spent along the meandering northern boundary of the Gulf Stream and the Slope Waters, and ends when the offspring reach the adult habitat on the continental shelf. Approximately one millimetre ML at hatching, *Illex* paralarva will grow a hundred fold in length, change from an epiplanktonic to a nektonic adult life-style and experience as much as 20°C decrease in environmental temperature as they reach coastal waters. Survival conditions during this period are mostly unknown. It has been argued that transition across food chain levels and to more

productive environments enables the species to attain their required growth. Provided with a limited yolk supply and energetically expensive life-style (O'Dor et al. 1986), temperature regime and food conditions may also impose serious limitations to survival during the early life.

Growth is related to size, feeding rates and temperature (Forsythe and van Heukelem 1987). Expressed as a function of size, growth variability may reflect environmental pressures and life history events (Werner 1988). In this chapter, size-specific growth of *I. illecebrosus* was reconstructed over a substantial part of the early life history and subadult life. The analysis included all the specimens available from preserved collections and the objectives were to assess, in the patterns of growth variation, the general effects of:

- (a) **ecological shifts**, associated with size-dependent changes in the form of the body (Okutani 1987; Nesis 1979a; Vidal 1994a);
- (b) **sexual differentiation**, which has effects on growth manifested as a pronounced size dimorphism in the adult life (Forsythe and van Heukelem 1987);
- (c) **environmental transitions**, mainly determined by the effect of temperature and food gradients across the Gulf Stream/Slope Water frontal system in individual growth performances. The analysis focuses on the understanding of common responses to main environmental pressures that will set the basis for the study of the environmental variability in the subsequent chapters.

3.2. Material and Methods

This study reconstructed the growth history from the gladii of 1393 preserved juvenile and 183 fresh-frozen sub-adult *I. illecebrosus* (mantle length larger than 100 mm) examined in the previous chapter (see Appendix 1 and Chapter 4 for a description of the samples' origins). In juvenile specimens, besides the weight (W) and the dorsal mantle length (ML), the following body dimensions were also measured, to 0.1 mm, following Roper and Voss (1983): Fin Length (FL), Eye Diameter (ED), Head Width (HW) and the Length of the Second Dorsal Arm (AII) as shown in Fig. 3.1.

3.2.1. Gladius analysis and numerical representation of growth

Gladius growth increments (GInc) were observed under a dissecting microscope and measured in micrometres using an Image Analysis System following the procedure described in Chapter 2. On each gladius, a series of GInc was reconstructed from the gladius anterior border towards the posterior end until the marks became faint (Fig. 2.1). 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: $0.25 \text{ GInc}_{i-1} + 0.5 \text{ GInc}_i + 0.25 \text{ GInc}_{i+1}$. This filter was designed, essentially, to average sharp differences between consecutive increments, likely caused by reading errors. Filtered GInc represented the gladius **Absolute growth rate** during one day (see chapter 2 for analysis of accuracy).

In order to analyze gladius growth variability in relation to size-dependent transitions during early life, GInc was expressed as a function of gladius length (GL) and mean size-specific growth curves were reconstructed by pooling GInc per 1 mm GL intervals. The analysis assumed that gladius growth variability is size- and not age-dependent.

The general effect of environment 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):

$$\text{DGP} = \text{FR} - \text{MR} \quad (3.1)$$

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

$$\text{MR}_i = 0.0043(W_i^{0.96})1.187^t \quad (3.2)$$

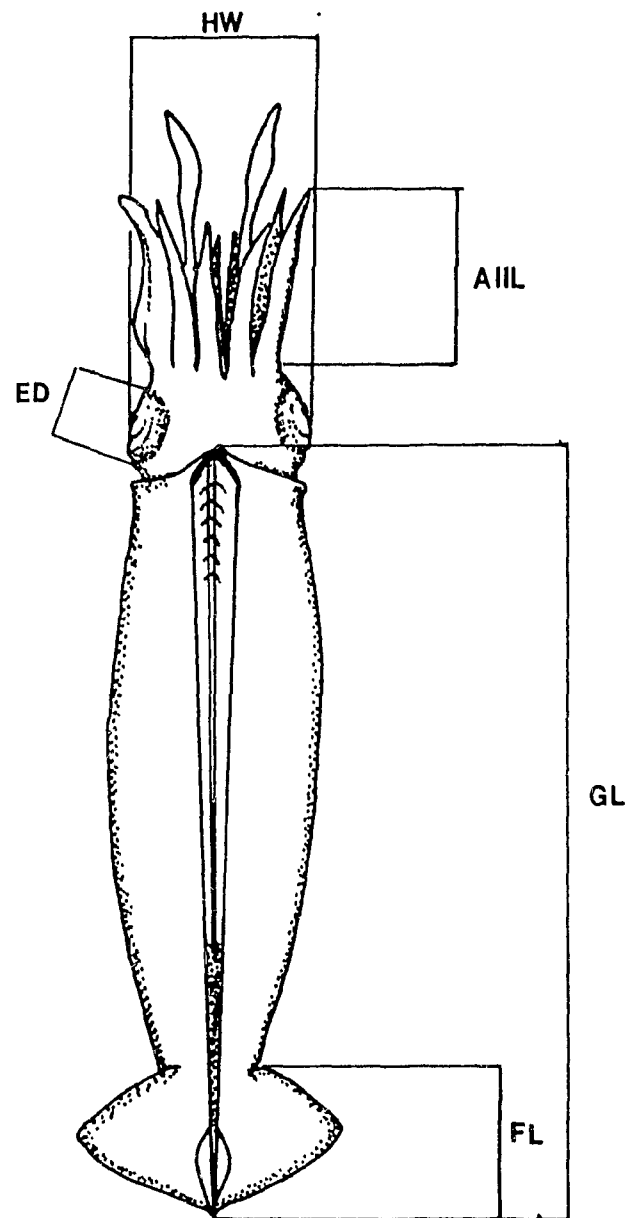


Figure 3.1. Dorsal view of juvenile *Illex illecebrosus* including the general form and position of the gladius. Body dimensions measured: A IIL, length of the second dorsal arm; ED, eye diameter; HW, head width; FL, fin length.

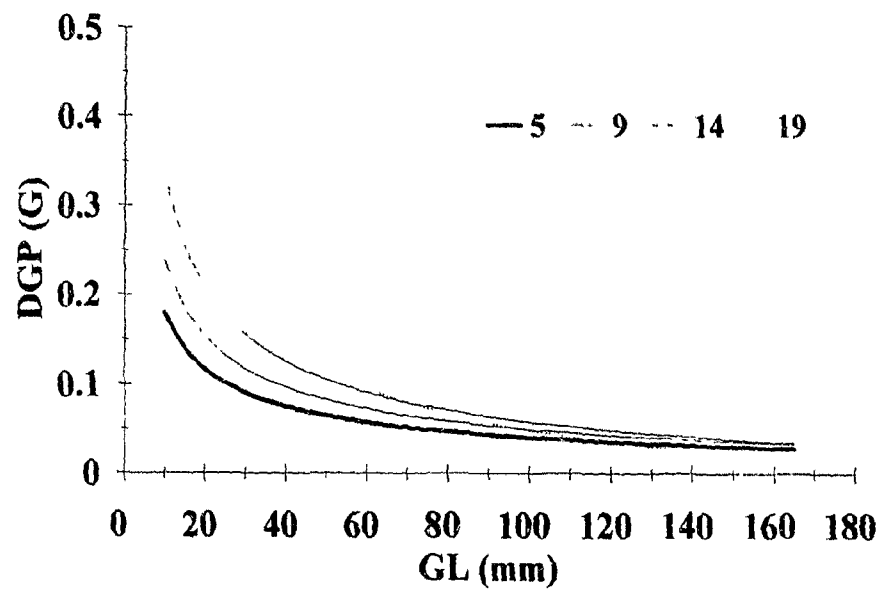


Figure 3.2. Variation of size- and temperature-specific daily growth potential, expressed as instantaneous growth rates (G), estimated by the energetic budget equation (O'Dor and Wells 1987). Temperatures in $^{\circ}\text{C}$ are indicated next to each line.

Table 3.1. Ontogenetic allometry between Log gladius length (GL) and the Log transformed: length of the second dorsal arm (AII), eye diameter (ED), head width (HW) and fin length (FL) in juvenile *Illex illecebrosus*. GL ranges in millimetres were defined according with the accepted points of discontinuity; slope represents the Log GL coefficient calculated by the linear regression (\pm SE). n , number of regression points; r^2 , coefficient of determination.

Relationship	GL range	n	slope \pm SE	r^2
Log GL x Log AII	6-32	690	0.908 ± 0.025	0.813
	32-99	610	1.108 ± 0.015	0.951
Log GL x Log ED	6-32	648	0.713 ± 0.030	0.682
	32-99	573	0.877 ± 0.022	0.854
Log GL x Log HW	6-32	765	0.645 ± 0.027	0.829
	32-99	307	0.852 ± 0.020	0.882
Log GL x Log FL	6-30	663	1.355 ± 0.042	0.785
	30-68	579	1.519 ± 0.021	0.947
	68-99	57	1.225 ± 0.109	0.833

$$FR_i = 0.058(W_i^{0.79})1.082^t \quad (3.3)$$

Assuming 1 Kcal g⁻¹, DGP estimates the potential absolute growth in grams per day (O'Dor and Wells 1987). Daily back-calculated GL were transformed into W_i by the relationship, $W = 0.000035 GL^{2.799}$ (see Chapter 2), and used to calculate size-specific DGP at different temperatures (Fig. 3.2).

Size- and temperature-specific "potential" and "observed" growth were compared after transforming DGP and GInc respectively into **Instantaneous Growth Rate** (*G*) by the equation:

$$G = 2.799(\ln GL_{i+1} - \ln GL_i) \quad (3.4)$$

for GInc, and the approximation ,

$$G = DGP_i/W_i \quad (3.5)$$

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

3.2.2. Growth Analysis

The effect of the development of sexual characters on growth was tested by a one-way analysis of covariance (ANCOVA) on GInc with SEX as the single factor and GL the covariate. Due to the effect of fixatives on the squid internal morphology, sex in juvenile squid could only be accurately determined in samples from the years 1985, 1989 (except sample 289) and 1991 (a total of 465 squids). For computation purposes the test was conducted in four GL intervals: (a) 10-40 mm GL; (b) 40-80 mm GL; (c) 85-120 mm GL; and (d) 120-160 mm GL). Each test was preceded by an analysis of homogeneity of slopes between the sexes (interaction GLxSEX).

3.2.3. Morphometric Analysis

Changes in body form were assessed using the allometric equation, $Y = aX^b$, where X was the GL and Y , the measured body dimensions (Fig. 3.1). The constants a and b represented the intercept and the constant of equilibrium of allometry, respectively, and were calculated by the linear regression of the log-transformed variables X and Y . In this model, $b=1$ indicated isometry, $b>1$ indicated positive allometry and $b<1$ negative allometry.

Points of discontinuity were visually determined in all GL vs body dimension plots and accepted only when the slopes calculated for data to the right and to the left were found to be significantly different. When the points of discontinuity were accepted, the parameters of the allometric equation were recalculated separately for each growth segment and the hypothesis of isometric growth ($b=1$) was tested. A test for homogeneity of slopes (covariance analysis) was employed to compare slopes in the same morphometric relationship (Zar 1984). The significance level adopted in all tests was 5%.

3.3. Results

3.3.1. Changes in body form

Relationships between the log-transformed body dimensions and gladius length are shown in Figure 3.3. Growth intervals, delimited by the accepted points of discontinuity, are summarized in Table 3.1. In all relationships, a point of discontinuity was detected at around 30-32 mm GL: AAIL, $F=50.11$ ($p<0.001$); ED, $F=19.41$ ($p<0.001$); HW, $F=38.62$ ($p<0.001$); FL, $F=6.15$ ($p=0.013$). Furthermore, a second marginally significant point of discontinuity was found in the allometric growth of FL at 69 mm GL ($F=4.01$, $p=0.046$).

In all growth intervals, body dimensions showed significant differences from isometric growth ($b=1$). Negative allometry was found in ED and HW; whereas positive

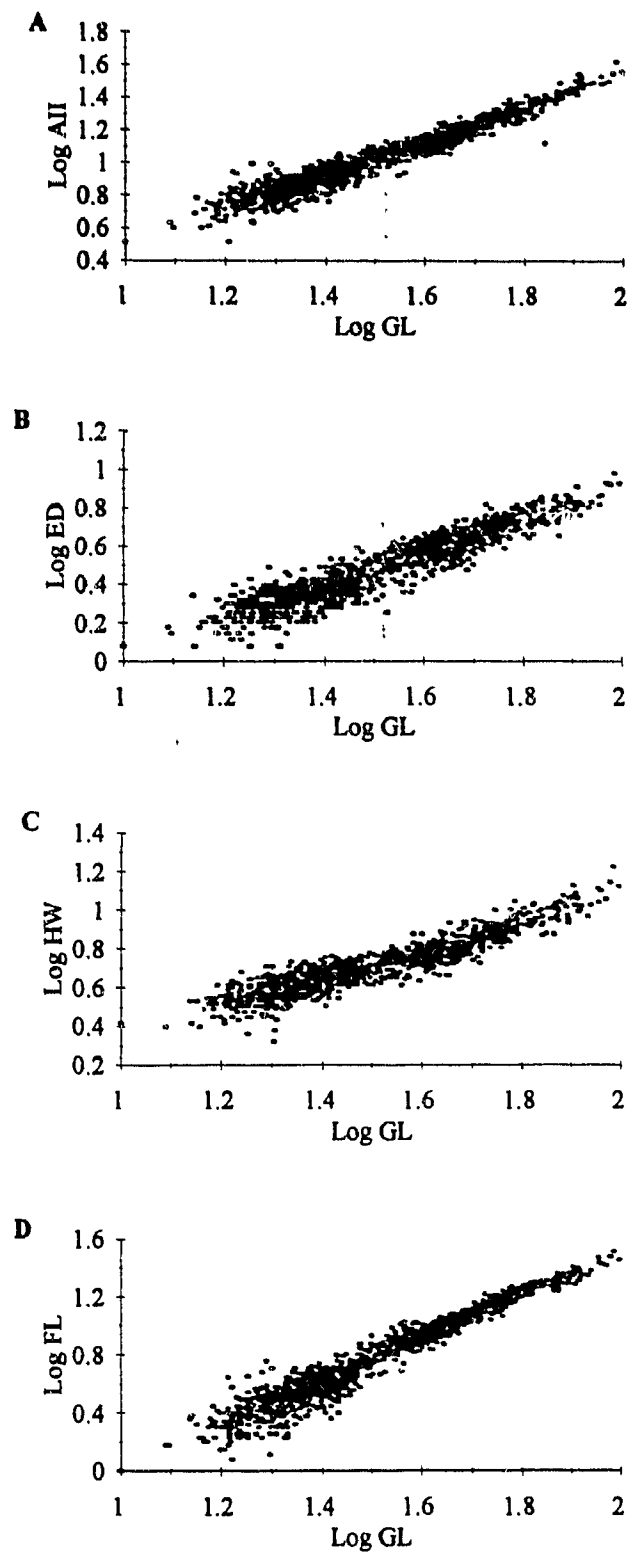


Figure 3.3. Ontogenetic allometry between Log Gladius Length (GL) and the Log-transformed body proportions: A, Length of the second dorsal Arm (AIL); B, Eye Diameter (ED); C, Head Width (HW); and D, Fin Length (FL) in juvenile *Illex illecebrosus*. The vertical dotted lines indicate the accepted points of discontinuity.

Table 3.2. Linear regressions of GInc on GL and test for the effect of sex differentiation in size-specific growth (ANCOVA). The analyses was conducted in four segments of the reconstructed size-specific growth curve (Fig. 3.5). Probability values are indicated for the sources of variance: sex groups (SEX), Gladius Length (GL) and the interaction between sex and GL (GLxSEX). *n*, the number of regression points (growth rates); *p*, probability value indicating the significance of the calculated slopes (slopes \neq 0, *t*-test).

GL mm		Regression				Ancova		
		<i>n</i>	interc.	slope	<i>p</i>	Sources		
						GLxSEX	SEX	GL
10-40	males	3081	0.209	0.007	<0.001	0.012	0.084	<0.001
	females	2394	0.200	0.007	<0.001			
	total	5479	0.205	0.007	<0.001			
41-80	males	1852	0.242	0.006	<0.001	0.012	0.413	<0.001
	females	1797	0.270	0.006	<0.001			
	total	3649	0.257	0.006	<0.001			
85-120	males	2591	0.933	0.000	0.125	0.535	0.052	0.011
	females	1958	0.972	-0.001	0.035			
	total	4549	0.951	-0.001	0.010			
121-160	males	2722	0.826	0.000	0.130	0.204	0.008	0.001
	females	2268	0.760	0.001	0.003			
	total	4990	0.794	0.001	0.001			

allometry was found in FL. AILL allometric growth changed from negative to positive after the 30 mm GL transition point (Table 3.1).

3.3.2. Early Growth History Reconstruction

The combined gladius growth increments of juveniles and adults (a total of 1576 squids) allowed the reconstruction of a mean size-specific growth curve for *I. illecebrosus* between 6 and 165 mm GL (Fig. 3.4). A two-phase trajectory was characterized, with size-specific growth increments increasing until 90 to 100 mm GL and stabilizing at around 0.8-0.9 mm in larger squids. Besides the increasing trend, four growth phases were further distinguished in juvenile growth rate variability, delimited approximately by the GL boundaries: 12, 31, 67 and 90 mm (Fig. 3.4). This pattern was consistently detected when the analysis was repeated with 50% and 25% of the data. Growth phases between 12-31 and 31-67 mm GL coincided with the growth intervals estimated by the morphometric analysis (Table 3.1). Growth phases under 12 mm GL and between 67 and 90 mm GL were less consistent because the number of growth increments available for these GL intervals was lower. A sharp increase in growth rates, however, was evident during the paralarval stages (GL < 10 mm) and during the late juvenile stage which precedes linear growth.

3.3.3. Development of sexual characters

Size-specific growth variation of males and females of both adults and juveniles is shown in Figure 3.5. The effect of size (GL) on GInc was significant in all size intervals (Table 3.2). In the juvenile phase (GL < 80 mm) the slopes of GInc regressed on GL varied between 0.006 and 0.007 ($p < 0.001$) and differed between males and females (GLxSEX, $p = 0.012$). In squids larger than 85 mm GL, GInc/GL slopes approximated zero and differences between sexes were not significant. The ANCOVA revealed significant differences of GInc between males ($0.887 \text{ mm} \pm 0.154 \text{ SD } n=2722$) and females (0.900

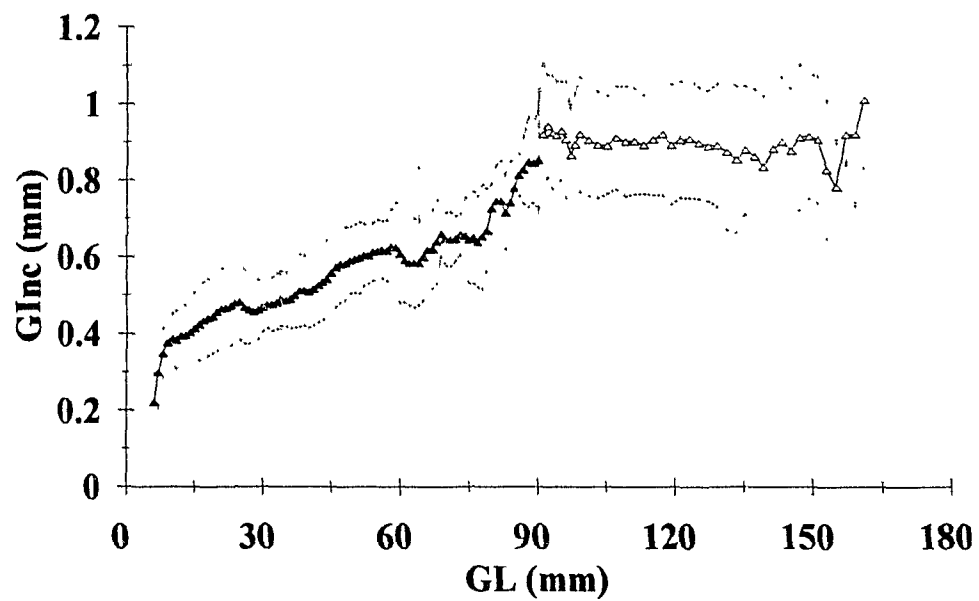


Figure 3.4. Mean size-specific growth curve reconstructed from the gladius analysis of *Illex illecebrosus*. Solid triangles, juveniles; Open triangles, sub-adults; upper and lower dotted lines indicate one standard deviation around the mean. Vertical dotted lines indicate the distinct growth phases.

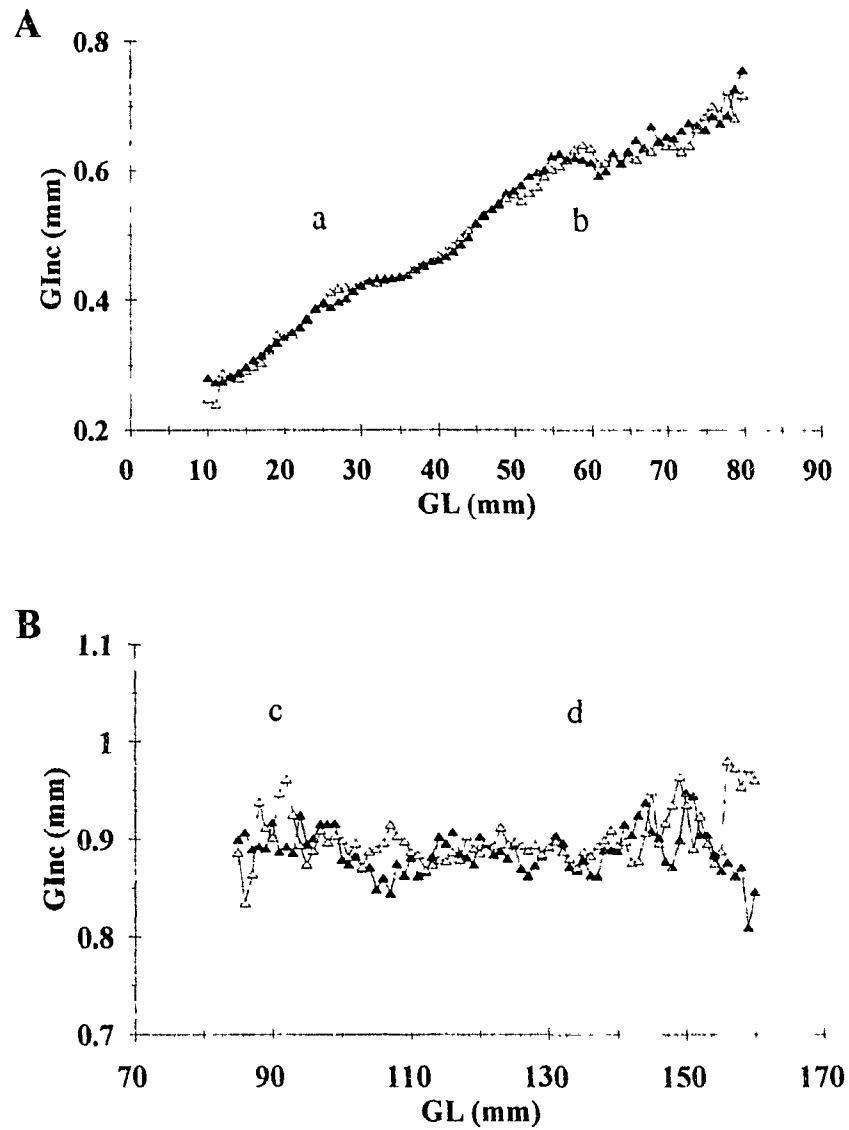


Figure 3.5. Mean size-specific growth curves reconstructed from the gladius analysis of juveniles (A) and sub-adults (B) of *Illex illecebrosus*. Solid triangles, males; Open triangles, females. Vertical dotted lines indicate the segments of the curve (a to d) compared by the Ancova (Table 3.2).

mm \pm 0.164 SD, $n=2260$) in the squids larger than 120 mm GL. In juveniles, such differences were not found, although the analysis was affected by the non-homogeneity of the slopes (Table 3.2).

3.3.4. Environment Transitions

The changes in mean variation of instantaneous growth rate with increasing GL is shown in Figure 3.6 in relation to the size- and temperature-specific growth potential (Fig. 3.2). 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 analyses was to evaluate the effect of the thermal gradient across the Gulf Stream and Shelf/Slope front in the individual growth performance. Since DPG are calculated for *ad libitum* food conditions, the wasted growth potential (expressed in percentage, Fig. 3.6) can also be thought of as being proportional to the amount of food required to achieve maximum growth. Despite their higher growth rates, juveniles living in the Gulf Stream (temperatures above 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%. On the shelf waters, during spring (at 5 to 6°C), subadults (GL >100 mm) grow at lower growth rates but are more efficient, wasting around 30 to 40% of their potential. Throughout the summer, as squids grow bigger and temperature increases on the shelf (Fig. 3.6), food-limitation increases.

3.4. Discussion

Ecological shifts

The initial interpretation of the size-specific growth variability deals with the description of growth trajectories. An increasing size-specific growth trend, possibly indicating an exponential GL growth trajectory, characterizes the juvenile "offshore" phase. At sizes larger than 90 - 100 mm GL, when squids are in the continental shelf

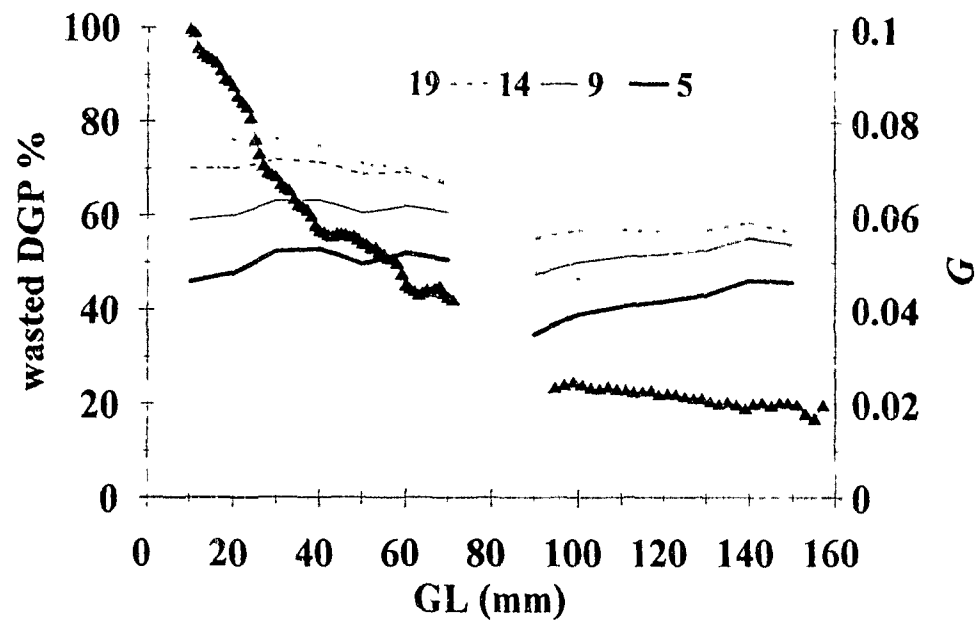


Figure 3.6. Mean size-specific instantaneous growth rate (G) variation (solid triangles) and percentile waste of growth potential (DGP) at different temperatures (lines). Temperatures in $^{\circ}\text{C}$ are indicated next to each line.

waters, growth is approximately linear. Similar gladius growth trajectories have been shown for the ommastrephids *Illex argentinus* and *Sthenoteuthis oualaniensis* (Bizikov 1991; Arkhipkin and Bizikov 1991). In the latter, an additional late phase of decreasing growth was associated with the later onset of sexual maturation (Bizikov in press). Size-at-age data have generally supported linear growth between 100 and 200 mm ML in *I. illecebrosus* and *I. argentinus* (Dawe and Beck 1992; Arkhipkin 1990; Rodhouse and Hatfield 1990 and others). For broader size ranges, size-at-age data have often indicated the necessity of more than one growth model (Jackson in press); and in some species, the exponential/linear combination has also been suggested (Bigelow 1992).

The maximum sizes observed for *I. illecebrosus* (around 340 mm ML), suggest that the juvenile growth phase extends through nearly one-third of the species' life cycle and this agrees with the pattern of extended juvenile life found in several cephalopod species (Jackson in press). In chapter 2, the transition from juvenile to adult growth mode in *I. illecebrosus* was found to occur at a smaller size (60-70 mm GL). This difference may be attributed to a discrepancy between methods of size-specific growth estimation; i.e. in the previous study, growth increments were not measured directly but estimated from the mean spacing of growth marks in fixed 10 mm gladius length intervals (Bizikov's "relative growth" method).

In the most consistent part of the reconstructed size-specific growth curve, two important growth phases were distinguished and separated at around 30 to 40 mm GL; a size interval which also marks a change in *Illex* body form. Such growth phases resembled the "hump-shaped" size-specific growth curves generated for organisms at transitional habitats or resources (Werner and Gilliam 1984) and can be interpreted according with Werner's "scaling" theory (Werner 1988). Changes of an organism's body form during ontogeny are associated with size increase (Gould 1966) and shifts of ecological niches. In each of the niches there may be an optimum size at which growth rate is maximized (hump-shaped curves). If selection tends to maximize growth across life history, ecological shifts would be expected at the sizes where these curves intercept. Thus distinct size-specific growth phases may represent squid growth at two consecutive

ecological niches. Where they intercept, at 30-40 mm GL (Fig. 3.4), a life-style transition and an ecological shift may take place (see below).

Morphological changes in ommastrephid squids during ontogeny generally consist of elongation of the body and enlargement of fins to deal with changing hydrodynamic factors, and the development of the raptorial apparatus (arms, suckers, tentacles, etc.; Nesis 1979b). In general, there is a planktonic paralarval stage (rhynchoteuthion stage) when the body is round, the arms poorly developed and the tentacles fused into a proboscis (Fig. 1.1.; Roper and Lu 1979; Vecchione 1979; Brunetti 1990; Vidal 1994a). The split of the proboscis and the elongation of the body characterizes the juvenile phase (Vidal 1994a), also associated with the transition from macroplanktonic to micronektonic life-styles (Nigmatullin 1987). Morphometric analysis of *I. argentinus* (Vidal 1994a), *Sthenoteuthis pteropus* (Nigmatulin 1987), and our data relate the latter transition to body form changes at around 25-28 mm ML (30-32 mm GL in *I. illecebrosus*) which seems to correspond to the ecological shift detected in the size-specific growth analysis (Fig. 3.4). Although less consistent in the size-specific growth data, paralarval growth seems to end at about 10 mm GL. This size approximates the size at the split of the proboscis (Vecchione 1979), but it precedes the transition estimated for *I. argentinus* based on the overall change in body form (Vidal 1994a).

Sexual differentiation

In *I. illecebrosus*, *I. argentinus*, *S. pteropus* and other ommastrephids, size differences between males and females are generally manifested in individuals larger than 150-200 mm ML (Arkhipkin and Scherbich 1991; Dawe and Beck 1992, Arkhipkin and Mikheev 1992). The differential growth between sexes in ommastrephids has been generally attributed to the early onset of male maturation (Arkhipkin and Scherbich 1991; Dawe and Beck 1992). Although our data suggest sex differences in the mean growth rates of squids larger than 120 mm GL, the relationship with male maturation is not clear. In a previous study using the same samples, spermiogenesis was observed in

only 2.4% of the males ($n=295$) and none had produced spermatophores (Perez and O'Dor in prep.). It is possible that preferential access to food through social interactions contributes to higher feeding rates among the faster growing females (Forsythe and Van Heukelem 1987). Such a behavioral mechanism might also explain the contradictory situation in loliginid squids where males grow larger.

Environmental transitions

In marine organisms, fast growth during the early pelagic stages generally increases chances of survival (Cushing 1975). Because squid growth is greatly enhanced as temperature and food ration increase (O'Dor et al. 1980, Forsythe and van Heukelem 1987) highest survival conditions should be associated with environments where both factors were maximized. The comparison between gladius growth increments and size- and temperature-specific potential growth suggests that, normally, juvenile *Illex* will not experience such environments. Instead, the 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 (O'Dor et al. 1986, Trites 1983, O'Dor and Balch 1985), the potential for growth is high but mostly wasted, possibly due to food limitation. Growth rate variation found in this study, particularly at small sizes, suggests that in the Gulf Stream, individuals could even be operating close to levels of starvation. Moving towards colder slope waters substantially decreases metabolic costs and feeding rates. Although the potential for growth is reduced, the cost of living is also lower and the risks of starvation are likely reduced. Maximization of growth, as required to enhance survivorship, likely depends on increasing food consumption. In spring, primary and secondary production are greatly enhanced in the Slope and Shelf waters (Mann and Lazier 1991). Thus, as juveniles penetrate into the adult habitat, favourable food conditions may compensate for less favourable temperature regime. A similar pattern has been conceptually shown by Brandt (1993), who also used an energetic model to assess

growth responses of larval fish to temperature and food gradients across fronts. The oceanographic structure influencing *Illex* early life, however, is not static. Fronts, and the thermal and food gradients associated with them, fluctuate spatially and temporally (Drinkwater et al. 1994). Biological production and temperature regimes vary geographically, seasonally and interannually (Mann and Lazier 1991). *Illex* offspring exposed to such variable conditions exhibit important intra- and interpopulational growth variations which may account for the variability of life history traits and be related with recruitment fluctuations. This questions will be addressed in the subsequent chapters.

On the continental shelf, the results presented in this chapter are comparable to a simulation study presented by O'Dor and Wells (1987). Subadults, experiencing typical surface temperatures in the spring (around 5-6°C), likely achieve most of their growth potential (Fig. 3.6). Throughout the summer, as surface temperatures increase and squids attain larger sizes, feeding requirements increase and food becomes limiting again. Estimates of food consumption from the Gulf of Maine to Cape Hatteras, indicate that the proportion of squids with empty stomachs and cannibalism tend to increase (up to 26%) in large animals towards the autumn (Maurer and Bowman 1985). Similar results were observed for the area off Nova Scotia and Newfoundland (Amaratunga 1983, Dawe and Brodziak in press) and also characterized the samples used for this analysis (Perez and O'Dor in prep.). In captivity, fed *ad libitum*, immature squids were shown capable of growing significantly faster than individuals in nature (O'Dor et al. 1980). However, the magnitude of this effect is unclear (O'Dor and Dawe in press) because the 1980 analysis assumed a stable population rather than constant turnover as is now known to occur (Dawe and Beck 1992). Food limitation, as feeding requirements increase (larger sizes, higher temperature), seems to vary seasonally and interannually (Dawe and Brodziak in press; Maurer and Bowman 1985).

CHAPTER 4. Small-scale horizontal variation in the growth of juvenile *Illex illecebrosus*.

4.1 Introduction

The environment experienced by the early stages of *Illex illecebrosus* is characterized by the dynamic interaction of distinct water masses of the northwest Atlantic (Fig. 1.2). The physical properties and the circulation patterns of such waters have been described by McLellan et al. (1953), McLellan (1957), Gatién (1976), Horne (1977), Csanady and Hamilton (1988) and others. Warm and dense waters of the northeast-flowing Gulf Stream and Sargasso Sea (temperatures and salinities above 15°C and 35‰, respectively) occupy the offshore area south of 40°N. Influenced by continental freshwater runoff and the southward flowing Labrador Current, Coastal Waters overlie the continental shelf exhibiting temperatures and salinities below 10°C and 35‰, respectively. Warm Slope Waters, of intermediate temperatures and salinities, flow northeast 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 seaward 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 seaward from the surface to depths of 800 to 1000 m. Shoreward, the shelf/slope front marks the encounter of warmer and more saline Slope Waters with colder and fresher Coastal Waters. The latter water mass extends over the Slope Waters at the surface and the front slopes down shoreward intercepting 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. 4.1) and reach maximum onshore positions annually during late summer and autumn (Drinkwater et al. 1994). Both fronts are also characterized, at surface, by irregularities related with the meandering behaviour of the Gulf Stream. Particularly important features, associated to 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 1988). In general, Coastal and Slope waters are more productive and particularly enhanced conditions occur at the fronts (Fournier 1977; Raymont 1980).

Early stages of *I. illecebrosus* concentrate throughout late winter, spring and summer along the inshore boundary between the Gulf Stream and adjacent Slope Water (Fedulov and Froerman 1980; Froerman et al. 1981; Amaratunga 1981; Dawe et al. 1982; Dawe and Beck 1985a and b; Rowell et al. 1985; Hatanaka et al. 1985; Rowell and Trites 1985). Size-distribution of squid in the area often varies widely, possibly reflecting (a) the protracted spawning season and (b) mechanisms of individual retention in the northeastern flowing Gulf Stream (Rowell and Trites 1985; Rowell et al. 1985); the entrainment of *Illex* into the Slope Water seems occur at different times throughout the year and in different places along the front. In the Slope Water, several broods of individuals may coexist and are subject to important horizontal gradients of food and temperature. As shown in the previous chapter, the decreasing temperature across the front reduces the potential for growth. The maximization of growth during early life, therefore, may depend on increasing feeding rates. In this chapter, growth conditions of squid groups distributed across the Slope Water are compared. The objective is to investigate the horizontal variability of juvenile growth in relation to the oceanographic structure and the associated spatial distribution of areas of food concentration off Nova Scotia during late winter and spring. The analysis will also address the relative importance of local variability in the seasonal juvenile growth which will provide a preliminary assessment of how much of the annual growth conditions can be reflected in juvenile samples collected in the Slope Water.

4.2. Material and Methods

4.2.1. Origin of samples and environmental data

This study was based on 26 samples of juvenile short-finned squid, *Illex illecebrosus*, collected during six research cruises conducted in the late winter and spring of 1979, 1981, 1982, 1988 and 1989 (Appendix 1). The area surveyed was bounded by latitudes 44° and 37°N and longitudes 66° and 52°W, extending from the Scotian shelf along the shelf break into the northern edge of the Gulf Stream (Fig.4.1).

In 1979, 1981 and 1982, the surveys were directed for *I. illecebrosus* and the main objective was to investigate the geographical and diel distribution of paralarvae and juveniles in relation with the hydrographic structure in the vicinity of the Gulf Stream and the shelf/slope fronts. Squids were caught by an Engles Midwater Trawl (1979-81) and a 510 Pelagic Trawl (1982) in tows distributed along north-south transects at 50, 100, 200, 300, 500 and 1000m depth strata. Details about sampling procedures and data collection are in 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 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 depth (Daphne Themelis, pers. com.).

Squid samples were fixed in formalin and preserved in ethanol (approximate concentrations: 10% and 70%, respectively), and were part of historical collections maintained at the Department of Fisheries and Oceans (St. John's - Nfdl, and Halifax - NS) and at the Atlantic Reference Centre (Huntsman Marine Biological Station, NB). When samples available 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 the gladius analysis (Appendix 1).

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 northwest 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 200m isobath) and the daily positions of the Gulf

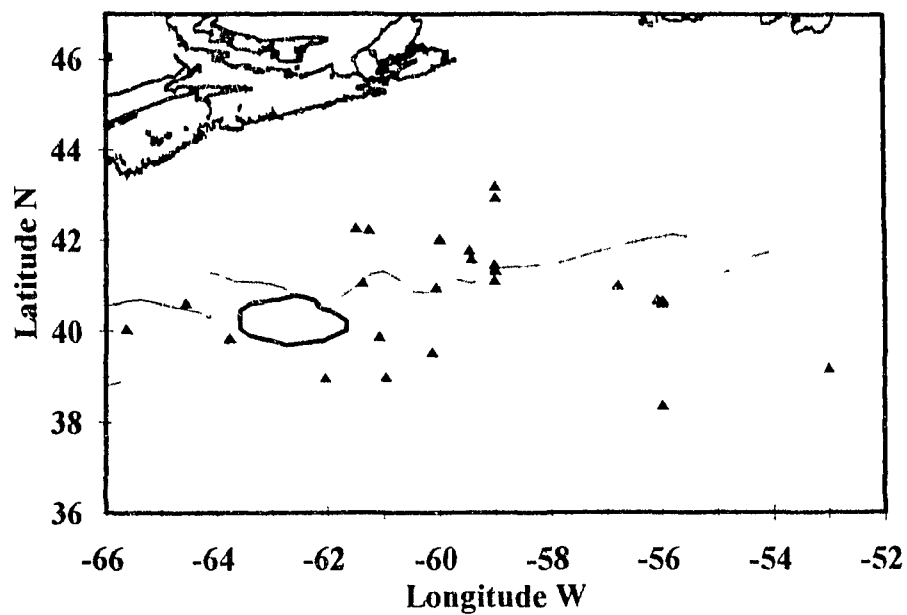


Figure 4.1. Study area and positions where juvenile *Illex illecebrosus* were sampled (solid triangles). The physical environment around the fishing stations was partially described by daily positions of the northern boundary of the Gulf Stream (dotted line), the shelf/slope front (solid line) and the Gulf Stream eddy activity (thick solid line) derived from NOAA satellite thermal imagery (Drinkwater et al. 1994). Latitudes and longitudes were decimal transformed.

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. 4.1). 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 the 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.

4.2.2. Recent growth analysis

The gladius analysis of preserved juveniles was conducted according to the methodology described in chapters 2 and 3. Series of individual growth increments were measured on the gladius structure and smoothed by a statistical filter. The 15 most recently deposited growth increments (Fig. 2.1) were used to describe the **recent growth** (RGI) of individual squid. In total, 1393 gladii were analyzed ranging from 21 to 102 per sample (Appendix 1).

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 in each survey. Because growth increments tend to increase as a function of gladius length during the juvenile phase (chapters 2 and 3), the "initial" gladius length back-calculated to 15 days before capture (GLi), was used as covariate. A test for the interaction between SAMPLES and GLi was carried out both between and within subjects (test of homogeneity of slopes) before each ANCOVA was performed. In all surveys this interaction was not found to be significant within subjects (Table 4.1). Between subjects, a marginal but significant

difference was found among the slopes of the 1982 samples (Table 4.1, $p=0.034$). 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 GLi. 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 Component 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, derived from the residuals obtained by the regression of RGI on GLi: RES, mean residuals of each sample; RANK, sample's rank within its survey (Table 4.2). 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 the association among samples.

4.3. Results

4.3.1. 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.4.2a-e). Samples of the 1981 survey were the most homogeneous in size and composed of the smallest squids (Fig.4.2b). Sharp size differences were characteristic among samples of the 1979 and 1989 surveys (Fig.4.2a and e); the latter included the largest squids analyzed in this study ($67.8\text{mm} \pm 12.8$ and $80.3\text{mm} \pm 7.6$, Mean \pm SD of samples 189 and 789 respectively).

Initial size (GLi), had a significant effect on RGI in all surveys (Between Subjects, Table 4.1). As a consequence, because samples differed in size-structure, higher mean growth profiles observed in each survey correspond to samples composed of larger squids (Fig. 4.3 and 4.2a-e). In the 1989 survey, growth profiles were also affected by GLi (Within Subjects, source DAYSxGLi, Table 4.1), and exhibited an increasing trend during the 15 days preceding capture (Fig. 4.3.e).

The ANCOVA on recent growth increments revealed highly significant differences among samples of all surveys but 1979 (Between Subjects, source SAMPLE, Table 4.1), where such differences were marginal ($p=0.048$). Recent growth profiles (Within Subjects, source DAYSxSAMPLE, Table 4.1) were only significantly different among samples of the 1982 survey ($p=0.029$). It is possible that this analysis was affected by the usage of filtered increments; this procedure tends to reduce the variance of the samples and could reinforce detectable differences among the samples compared. However, even the more conservative significance level, $\alpha=0.01$, gave significant differences among samples of all surveys, except 1979.

Pairwise comparisons, performed by the Tukey test on residuals of RGI regressed on GLi (Fig. 4.2f-j), indicated results generally independent of the size-structure of the samples (Fig. 4.2 a-e). The analysis of residuals in samples of the 1982 survey produced inconclusive results (Fig. 4.2h) and was possibly affected by the different slopes (Table 4.1).

4.3.2. Spatial distribution and main environmental features in relation with juvenile *Illex* recent growth condition.

Qualitative analysis.

A description of the growth variability found among the samples in relation to their geographic distribution and relevant environmental features is given below. In figures 4.4-4.8, the positions of the fishing stations where *Illex* were caught are shown in relation to the daily locations of the shelf/slope front, the northern boundary of the Gulf

Table 4.1. Comparison of juvenile *Illex illecebrosus* recent growth 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 considered as repeated measures within each squid gladius) among samples examined in each survey. SAMPLE was the grouping factor; DAYS was the time period during which RGI was repeatedly measured (15 growth increments or "days") and GLi was the covariate that represented the GL at the beginning of the measured growth period. The analysis was preceded by a test of homogeneity of slopes, where the interaction between SAMPLE and GLi was tested. Significant *p*-values (*p*>0.05) are printed in bold. Degrees of freedom (df), mean squares (MS), and F ratios are also indicated.

Sources	1979 df	MS	F	<i>p</i>	1981 df	MS	F	<i>p</i>	1982 df	MS	F	<i>p</i>	1988 df	MS	F	<i>p</i>	1989 df	MS	F	<i>p</i>
Homogeneity of slopes																				
<i>Between Subjects</i>																				
SAMPLE × GLi	1	0.009	0.358	0.551	1	0.021	0.575	0.449	1	0.089	4.285	0.039	1	0.302	2.923	0.091	1	0.086	2.704	0.101
<i>Within Subjects</i>																				
DAYS × SAMPLE × GLi	14	0.001	0.658	0.817	14	0.002	1.115	0.338	14	0.001	0.723	0.753	14	0.002	0.542	0.909	14	0.002	1.069	0.381
Ancova																				
<i>Between Subjects</i>																				
SAMPLE:	4	0.059	2.458	0.048	4	3.060	122.287	<0.001	5	0.164	8.738	<0.001	2	0.694	7.751	0.001	6	0.831	26.701	<0.001
GLi	1	0.340	14.257	<0.001	1	0.225	9.002	0.003	1	1.461	77.880	<0.001	1	0.975	10.892	0.001	1	21.200	681.174	<0.001
<i>Within Subjects</i>																				
DAYS	14	0.001	0.622	0.849	14	0.001	0.636	0.837	14	0.001	0.571	0.889	14	0.002	0.560	0.897	14	0.007	4.653	<0.001
DAYS × SAMPLE	56	0.001	0.565	0.796	56	0.002	0.777	0.887	70	0.002	1.349	0.029	28	0.003	0.667	0.906	84	0.001	0.762	0.947
DAYS × GLi	14	0.001	0.785	0.687	14	0.001	0.602	0.866	14	<0.001	0.269	0.997	14	0.003	0.751	0.723	14	0.024	15.636	<0.001

Figure 4.2. Mean gladius length (A to E, bars) and mean residual recent growth (F to J, symbols) of the analyzed samples. Residuals were calculated from the regression of RGI on GLi. Samples are sorted from left to right in ascending order of mean GL. Error bars represent one standard deviation. Capital letters on top of bars and symbols indicate the result of the Tukey test in a descending order; samples labelled with the same letters were not found to be significantly different. Samples not labelled could not be distinguished from the others by the test. A and F, 1979 survey; B and G, 1981 survey; C and H, 1982 survey; D and I, 1988 survey; E and J, 1989 survey.

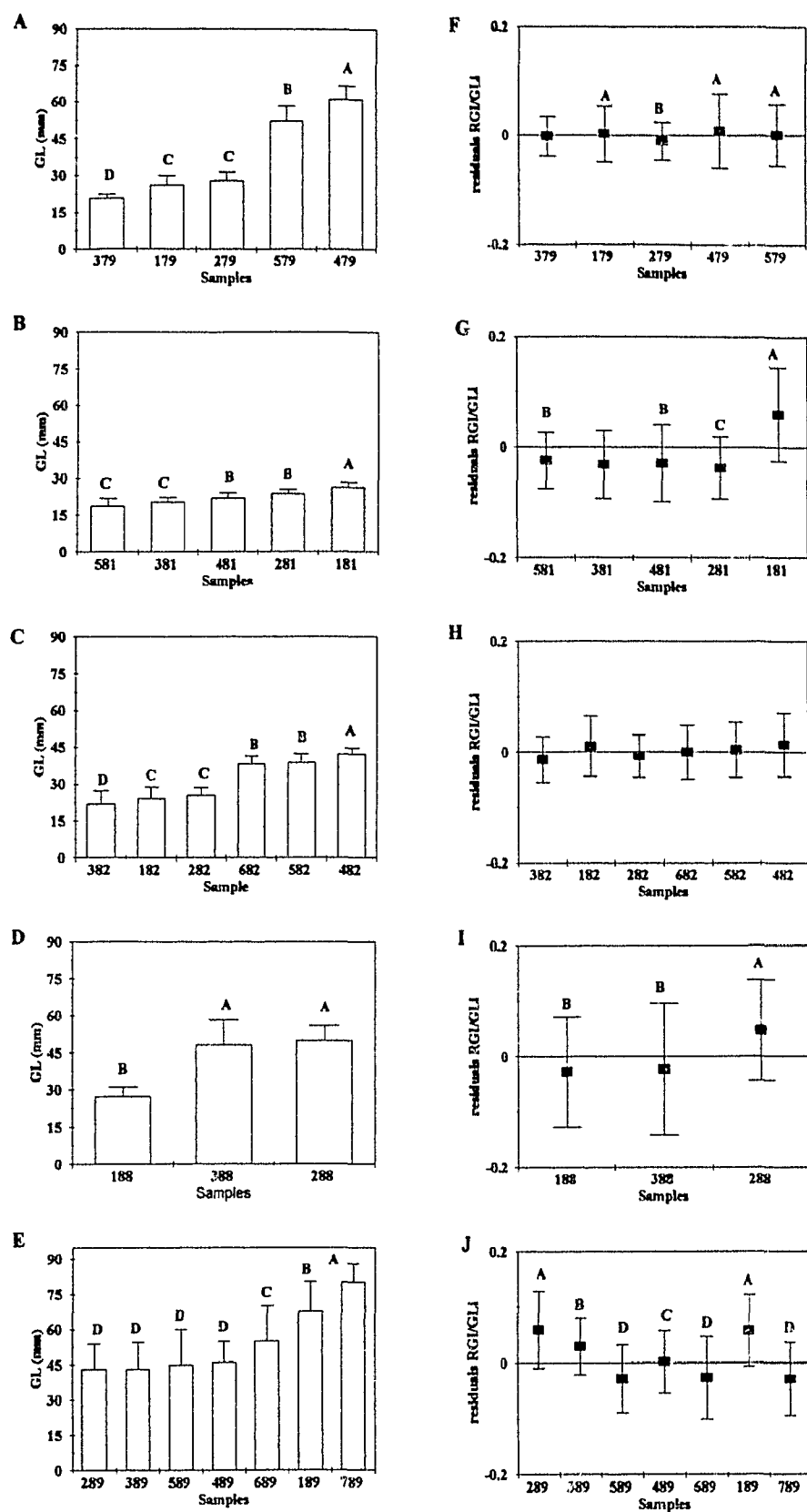


Figure 4.2.

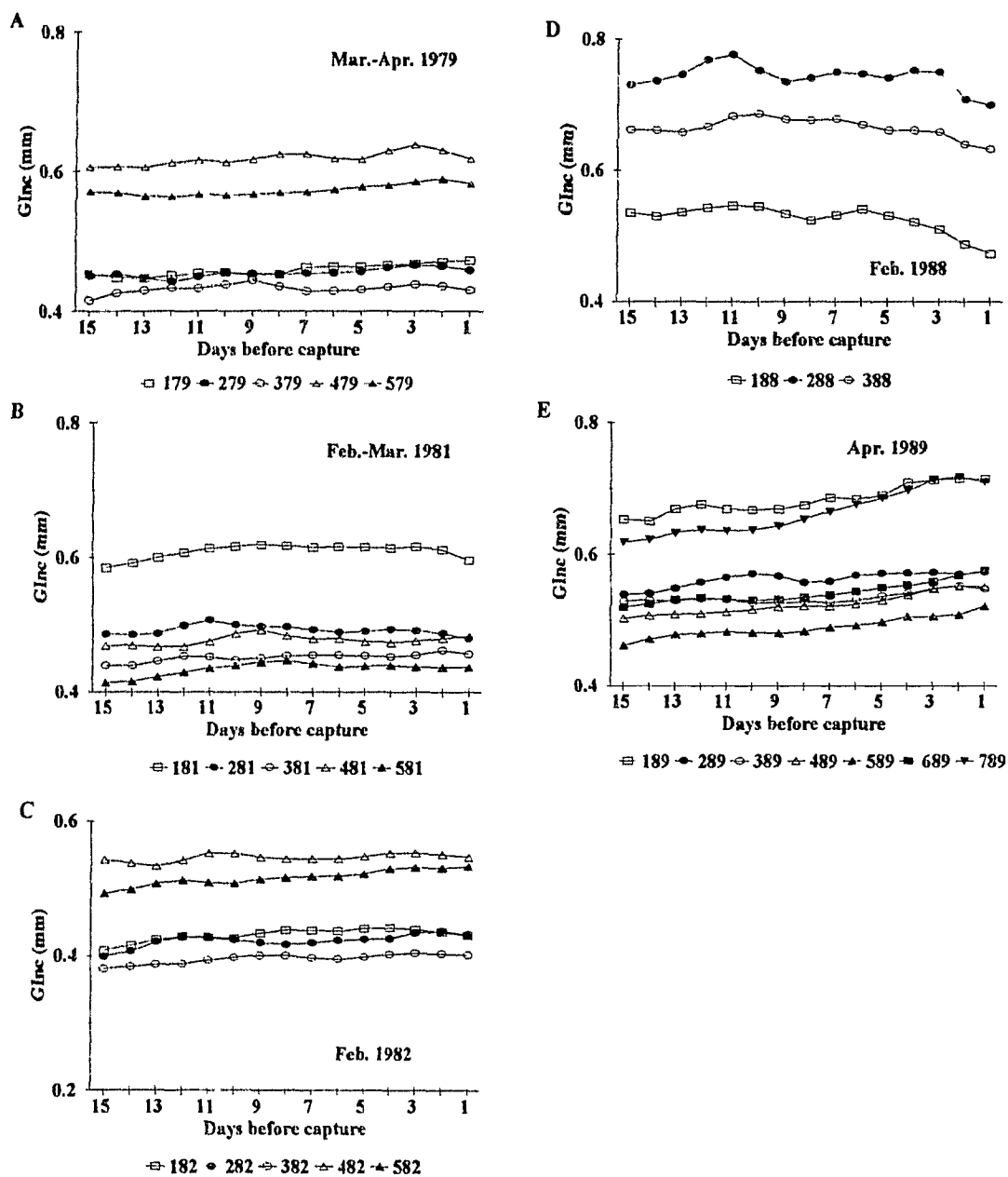


Figure 4.3. Mean recent growth profiles of the analyzed squid samples as reconstructed from the gladius structure. A, 1979 survey; B, 1981 survey; C, 1982 survey; D, 1988 survey; E, 1989 survey.

Stream and Gulf stream eddies. Appendices 2 to 7 show vertical temperature and salinity profiles available for the fishing transects.

March 1979

Two consecutive surveys combined (Appendix 1) covered a wide longitudinal range (65°-53°W). Juvenile *Illex* were caught at temperatures ranging from 4.81 to 18.69°C and were particularly abundant in the Slope Water and Gulf Stream at temperatures higher than 11°C (Amaratunga et al. 1980). Samples 479 and 579 were caught within warm Slope waters; the former in the vicinity of shelf/slope front (Fig. 4.4 and appendix 2). Samples 179, 279 and 379 were the westernmost samples examined in this study and originated from an area where the shelf/slope front and the Gulf Stream boundary were particularly close². Samples 379 and 279 were caught at the shelf/slope front and the boundary of the Gulf Stream respectively (Fig. 4.4 and Appendix 2). Growth variability among these samples was minor. Significantly lower recent growth condition was found in sample 279 (Fig. 4.2a).

February-March 1981

The transects of this survey covered an easterly area off the coast of Newfoundland within the boundaries 41°44'-37°16'N and 56°00'-47°00'W. Catches of juvenile *Illex* along the four transects were higher in stations under the influence of warm Slope Water and at the boundary of the Gulf Stream (Dawe et al. 1981, Dawe and Beck 1985). Samples 281, 381 and 481 were collected during a 24-hours station and their location was better represented by the temperature and salinity profiles along the fishing transect (Appendix 3). Sample 381 was caught in a 1000 m deep tow at 9°C under the influence of Labrador Slope Waters. Sample 281 was caught at the surface layer within an intrusion of the Gulf Stream and 481 was caught deeper within the warm Slope Water.

²Temperature and salinity profiles for the transect where sample 179 was caught were not available. Since this station was located in the vicinity of 279 and 379, surrounding conditions were assumed to be similar.

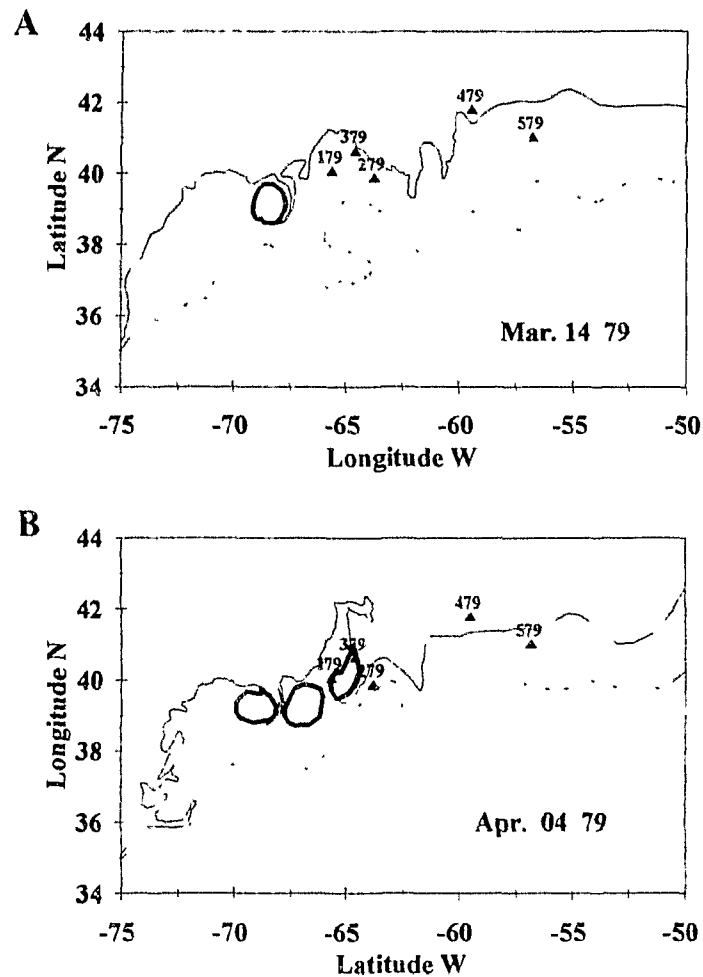


Figure 4.4. Positions where the analyzed samples were collected in the 1979 survey (solid triangles) in relation to the nearest available daily positions of the boundary of the Gulf Stream (dotted line), the shelf/slope front and warm-core rings (thick line). Dates are indicated at the bottom right corner of panels A and B. The dates of sample collection are: Sample 179, Mar. 10; Sample 279, Mar. 16; Sample 379, Mar. 17; Sample 479, Apr. 3; Sample 579, Apr. 5. Latitudes and longitudes were decimal transformed.

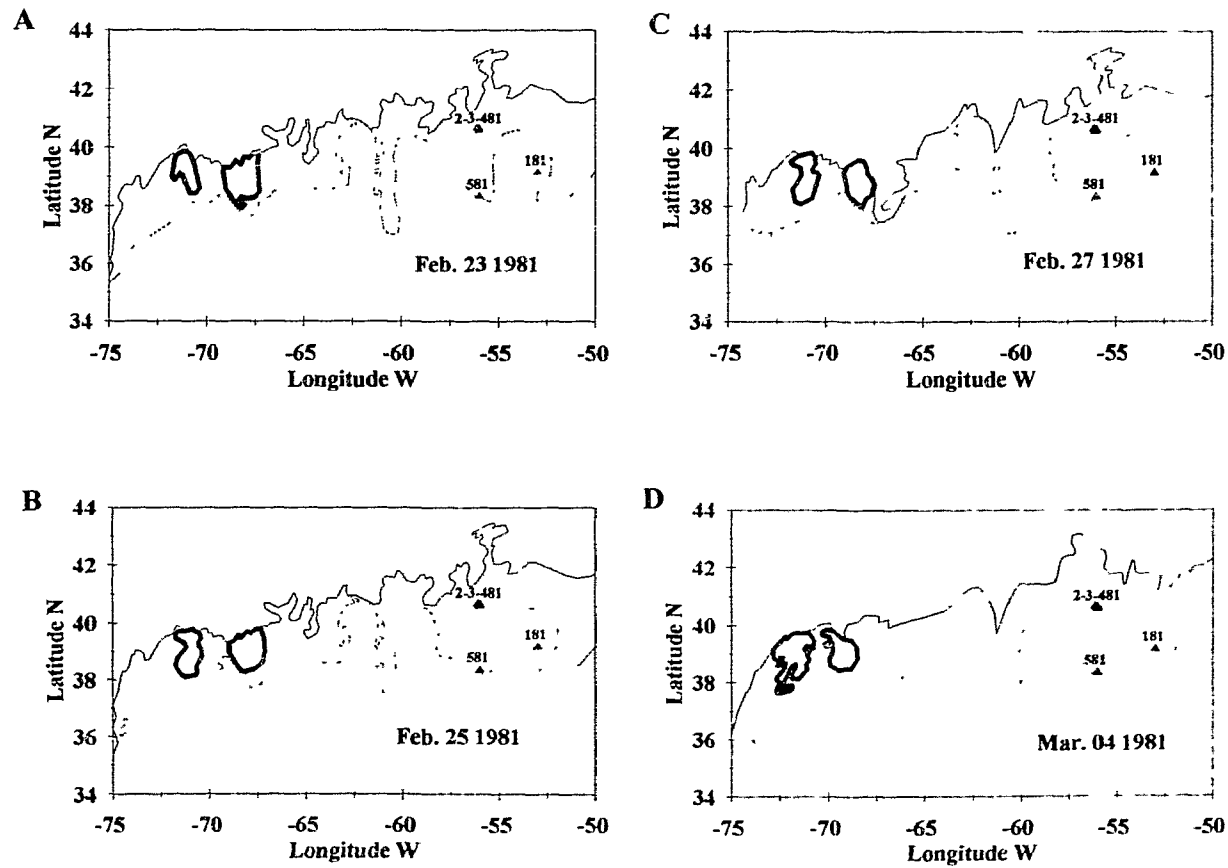


Figure 4.5. Positions where the analyzed samples were collected in the 1981 survey (solid triangles) in relation to the nearest available daily positions of the boundary of the Gulf Stream (dotted line), the shelf/slope front and the warm-core rings (thick line). Dates are indicated at the bottom right corner of the panels A to D. The dates of sample collection are: Sample 181, Mar. 3; Sample 281, Feb. 25; Sample 381, Feb. 24; Sample 481, Feb. 25; Sample 581, Feb. 27. Latitudes and longitudes were decimal transformed.

Samples 181 and 581 were part of large *Illex* catches that occurred near the boundary of the Gulf Stream (Fig. 4.5). The lowest and the highest recent growth conditions corresponded to samples 281 and 181, both under the influence of Gulf Stream waters (Fig. 4.2b).

February 1982

The sampling was conducted within 59°-63°W and from the edge of the Scotian Shelf southward to 38°N. During the survey, the area was characterized by an intense Gulf Stream eddy activity (Fig. 4.6). Most of the *Illex* catches occurred at the boundary of the Gulf Stream and the warm Slope Water in temperatures ranging from 12.1° to 16°C (Amaratunga and Budden 1982). The samples analyzed were located within warm Slope Waters between two Gulf Stream eddies (Fig. 4.6 and Appendix 4). Relatively superior growth was observed in squids from samples 482 and 182. The former was caught near the shelf/slope front and the latter in the periphery of a Gulf Stream ring (Fig. 4.6). Lowest growth residuals were exhibited by sample 582 which came from waters near the Gulf Stream boundary.

February 1988

The survey covered the area between 59° and 64° W and from the 100 m isobath to the northern boundary of the Gulf Stream. Juvenile *Illex* specimens in this survey were scarce. For the gladius analysis, samples 188 and 388 were composed of squids caught in three neighbouring stations each (Appendix 1). All samples were collected in the vicinity of the shelf/slope front (Fig. 4.7; Appendix 5). For samples 188 and 288, in particular, vertical profiles indicate the influence of the shelf waters at the surface layer overlying the warm Slope waters (Appendix 5). Because the oblique tow sampled mostly deeper layers (D. Themelis pers. com.), it is likely that the squids were caught in the warm Slope Water. Sample 288 was the northernmost and exhibited the highest recent growth (Fig. 4.2).

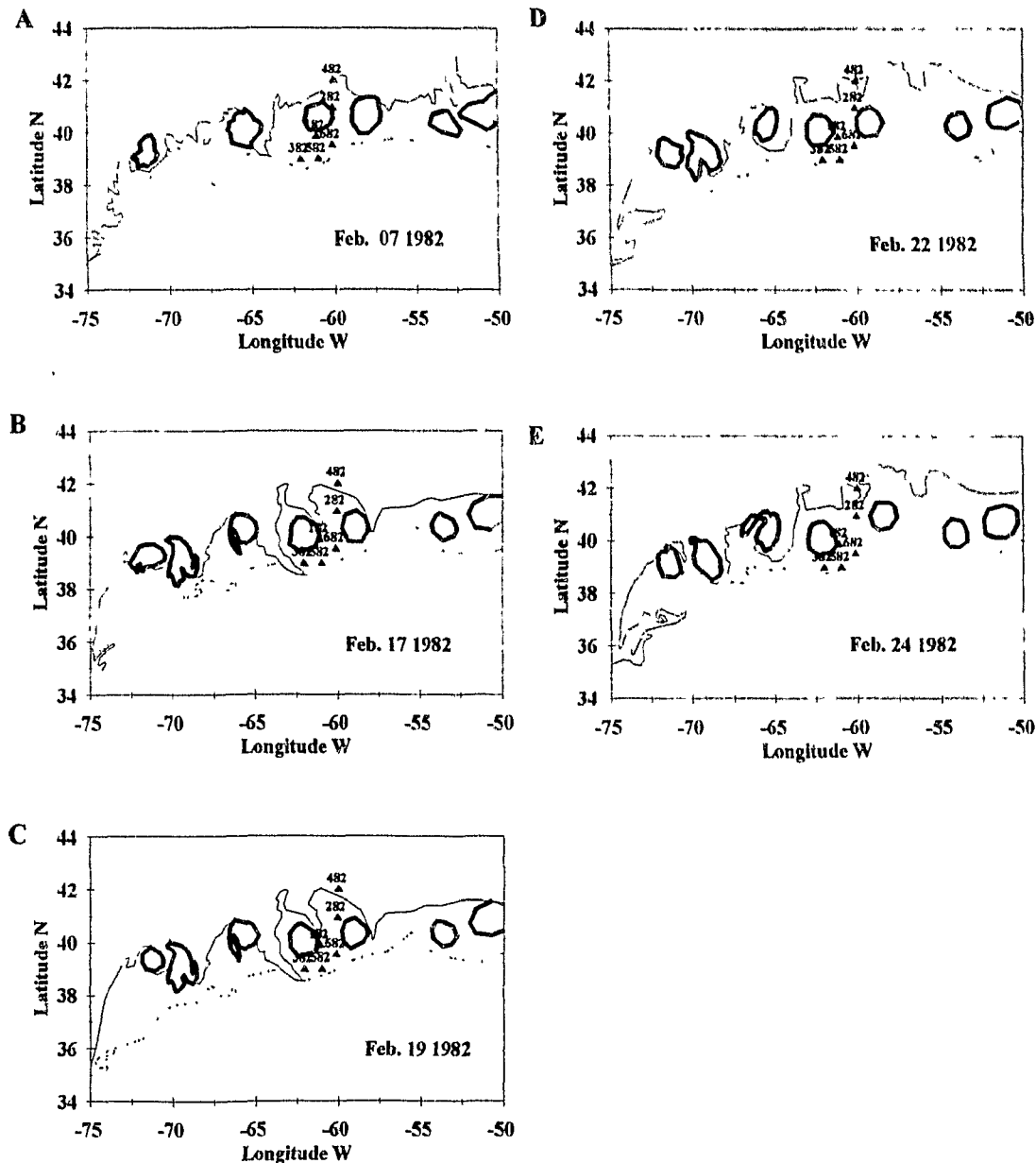


Figure 4.6. Positions where the analyzed samples were collected in the 1982 survey (solid triangles) in relation to the nearest available daily positions of the boundary of the Gulf Stream (dotted line), the shelf/slope front and warm-core rings (thick line). Dates are indicated at the bottom right corner of the panels A to E. The dates of sample collection are: Sample 182, Feb. 17; Sample 282, Feb. 23; Sample 382, Feb. 7; Sample 482, Feb. 23; Sample 582, Feb. 18; Sample 682, Feb. 21. Latitudes and longitudes were decimal transformed.

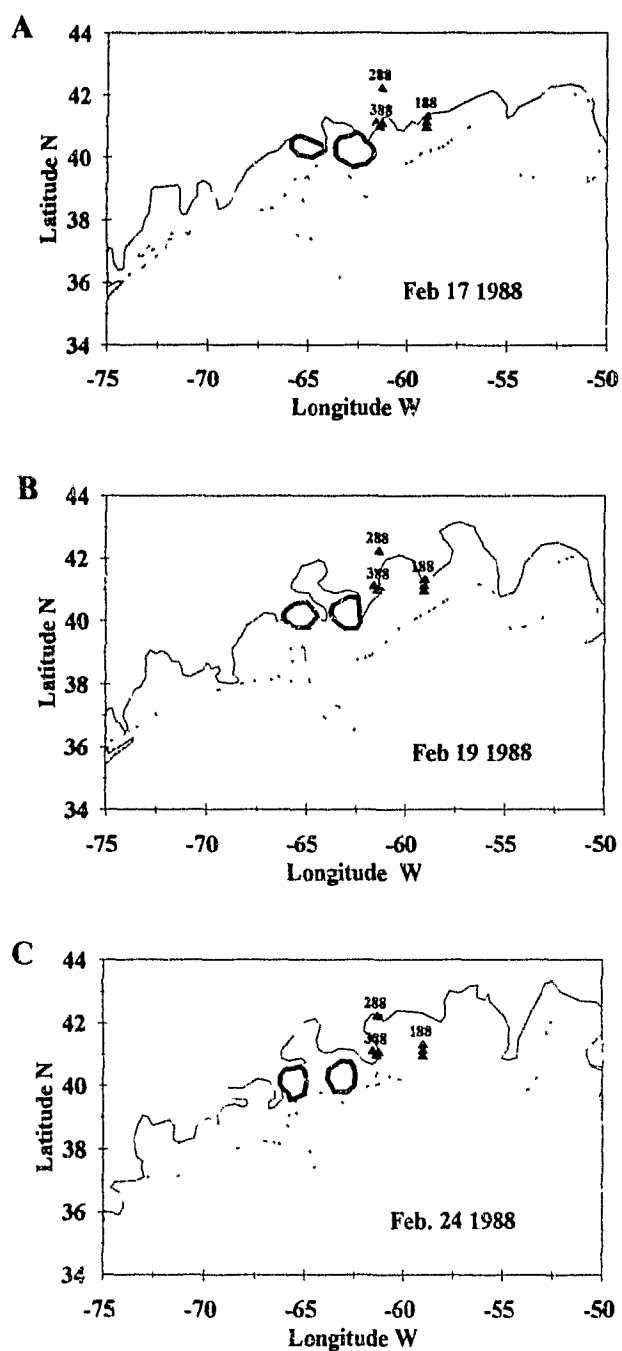


Figure 4.7. Positions where the analyzed samples were collected in the 1988 survey (solid triangles) in relation to the nearest available daily positions of the boundary of the Gulf Stream (dotted line), the shelf/slope front and warm-core rings (thick line). Dates are indicated at the bottom right corner of the panels A to C. The dates of sample collection are: Sample 188, Feb. 18; Sample 288, Feb. 23; Sample 388, Feb. 23. Latitudes and longitudes were decimal transformed.

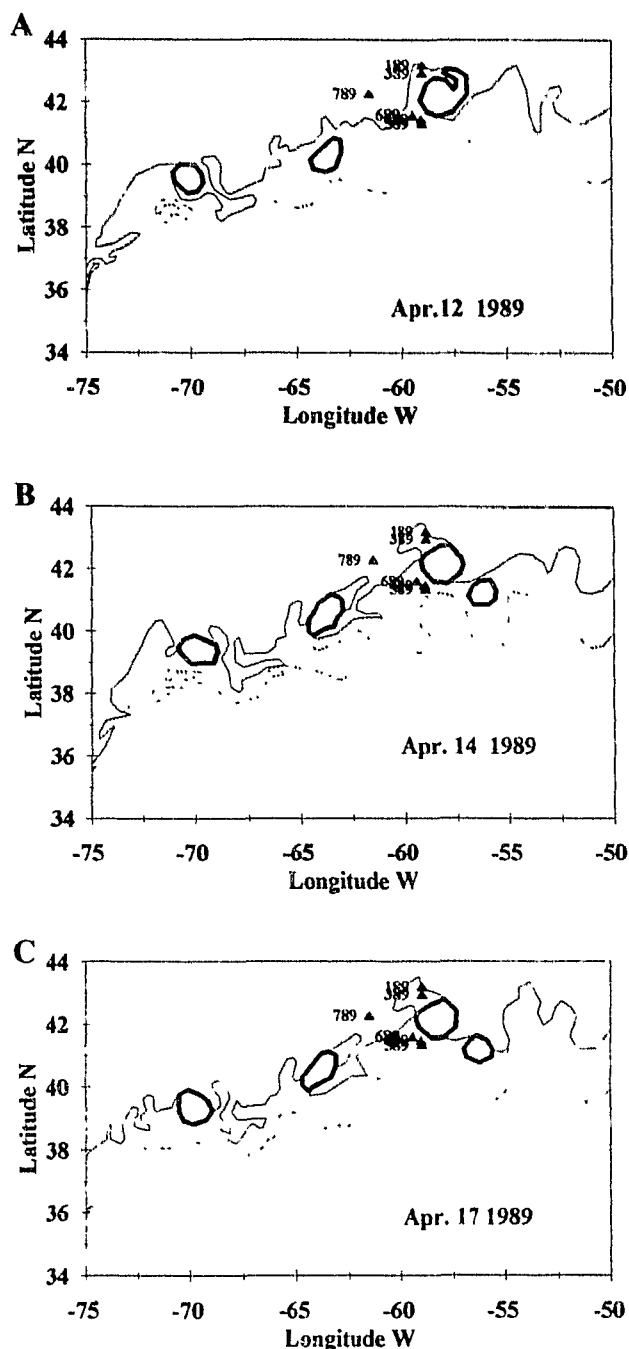


Figure 4.8. Positions where the analyzed samples were collected in the 1989 survey (solid triangles) in relation to the nearest available daily positions of the boundary of the Gulf Stream (dotted line), the shelf/slope front and warm-core rings (thick line). Dates indicated at the bottom right corner of the panels A to C. The dates of sample collection are: Sample 1-289, Apr. 12; Sample 389, Apr. 13; Sample 489, Apr. 13; Sample 589, Apr. 14; Sample 689, Apr. 14; Sample 789, Apr. 17. Latitudes and longitudes were decimal transformed.

April 1989

The area covered by the 1989 survey (the same as the preceding year) was characterized by intense meander and eddy activity at both oceanographic fronts (Figure 4.8). The highest recent growth was observed in squids of samples 189-289 (replicates) and 389 (Fig. 4.2j). These samples were collected in close association with the shelf/slope front and with the periphery of a warm core eddy (Fig. 4.8). Growth was lower in samples 489, 589 and 689 caught southward, between the same eddy and the boundary of the Gulf Stream; and in sample 789 collected westwards, onshore the shelf/slope front (Fig. 4.8).

Multivariate analysis

The analysis of principal components generated a bi-dimensional representation of the relationship between variables and samples (Fig 4.9). The association among samples was analyzed from the scores produced by the first two calculated factors that explained 66.5% of the total variance (Table 4.2). Factor 1 was mainly defined by geographic and environmental components (higher positive and negative weighting, Fig. 4.9.a, Table 4.2). Considering the graphic representation in figure 4.9, southerly samples positioned close to the Gulf Stream boundary and collected at higher temperatures, should be placed on the right hemiplane. Northerly 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. 4.9.a, Table 4.2). Scored by this factor, easterly 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, shows a concentration of samples with superior growth conditions in the second quadrant (Fig. 4.9.b). This pattern indicates that within each survey, the squids with higher recent growth increments tended to be found: in (a) northeasterly 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 of the first

Table 4.2. Analysis of the association between growth, the horizontal distribution of juveniles and main oceanographic features. A Principal component analysis was employed including: temperature in degrees celsius (TEMP); decimal latitudes (LAT) and longitudes (LONG); distances in kilometres 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 x GLi (RES); growth rank of each sample within its survey (RANK). Values shown for all variables are not standardized. The positive and negative signals of the distances (except DNE) refer to their onshore/offshore positions. The linear coefficients of the variables in the first three factors rotated by the PCA are indicated in the last three rows. The eigenvalues and the amount of variance explained (in %) by each factor, including the first two used for the analysis (in bold), are indicated in the last two columns.

Samples	Variables									Eigenvalues	Variance explained %
	LAT	LONG	DSH	DGS	DSF	DNE	TEMP	RES	RANK		
179	40 07	65 63	-232 91	213 35	-136 70	194 46	15 0	0 003	2		
279	39 87	63 78	-201 24	97 78	-52 63	364 84	16 6	-0 011	5		
379	40 63	64 57	-326 29	130 38	-14 1	333 36	15 2	-0 002	4		
479	41 80	59 47	-204 79	236 35	-63 63	447 41	11 8	0 008	1		
579	41 02	56 80	-400 61	137 05	-45 58	664 87	13 8	0 000	3		
181	39 20	53 00	-750 86	-106 67	-212 28	1380 72	15 1	0 059	1		
281	40 63	56 02	-481 21	134 03	-95 91	1007 49	15 8	-0 038	5		
381	40 70	56 10	-475 06	127 97	-76 91	1001 75	9 0	-0 031	4		
481	40 68	56 00	-483 28	136 31	-96 60	1011 93	13 2	-0 029	3		
581	38 38	56 00	-694 13	30 37	-234 69	1024 53	19 1	-0 024	2		
182	39 90	61 08	-397 07	148 90	-58 47	8 79	15 5	0 010	2		
282	40 96	60 07	-301 64	192 24	-54 86	50 67	11 4	-0 007	5		
382	39 00	62 03	-473 67	58 89	-163 75	145 25	15 2	-0 013	6		
482	42 03	60 00	-177 53	290 76	15 97	149 12	13 0	0 013	1		
582	39 02	60 96	-516 10	41 11	-157 90	96 49	14 0	0 004	3		
692	39 55	60 13	-448 37	65 56	-175 94	66 52	13 2	-0 000	4		
188	41 13	59 02	-305 04	129 81	-20 41	279 93	13 3	-0 028	3		
288	42 25	61 27	-169 31	174 46	-19 69	185 18	12 1	0 047	1		
388	41 08	61 38	-316 69	44 17	39 76	103 32	11 0	-0 023	2		
189	43 22	59 00	-66 69	200 02	-11 11	63 89	11 0	0 058	2		
289	43 22	59 00	-66 69	200 02	-11 11	63 89	11 0	0 059	1		
389	42 96	59 00	-96 43	189 48	-17 59	47 23	12 0	0 030	3		
489	41 48	59 02	-271 89	21 37	-84 78	41 59	12 0	0 002	4		
589	41 35	59 00	-280 73	28 48	-105 56	56 99	12 0	-0 028	6		
689	41 62	59 43	-302 65	38 95	-81 12	103 80	11 0	-0 027	5		
Factors											
1	0 962	-0 727	0 856	0 697	0 652	-0 877	-0 461	-0 304	0 088	4.179	46.435
2	0 053	0 112	0 052	0 384	-0 031	0 246	-0 551	0 743	-0 849	1.805	20.051
3	-0 078	0 121	0 207	-0 360	0 584	-0 336	0 641	0 369	-0 352	1.318	14.645

Table 4.2

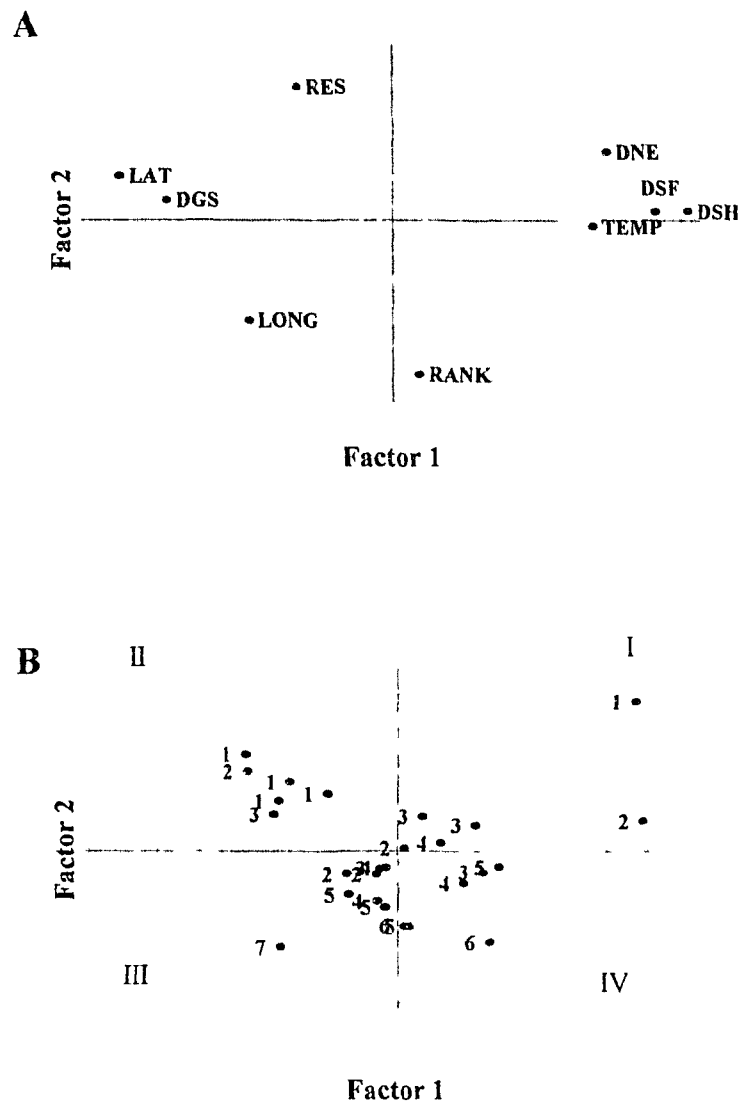


Figure 4.9. Spatial representation of geographic, environmental and growth variables (A), and of samples (B), scored by the first two factors obtained from the Analysis of Principal Components. Factor 1 (horizontal axis) explained 46.4% of the variance and Factor 2 (vertical axis) explained 20%. In panel B, samples are labelled by their ranks within each survey. Dotted line surrounds a group constituted mainly of samples with superior growth. Roman numbers indicate the four quadrants.

quadrant, diverged from the main pattern. In spite of its high growth and the easterly position (the easternmost of all samples analyzed), 181 was collected offshore the Gulf Stream boundary at a great distance from the shelf (Figure 4.5).

4.5. Discussion

Spatial variability in squid growth has been reported from statolith-determined size-at-age data (Arkhipkin and Scherbich 1991; Arkhipkin and Nekludova 1994). In general, these results referred to cumulative growth differences of individuals in distinct geographic areas during most of their life cycle. In the present study, recent growth, reconstructed from the gladius structure, was employed to investigate small-scale spatial growth variability during a particular phase of the life cycle. The analysis required special caution with respect to the effect of size in growth increment variation (Campana and Jones 1992). Growth increments have been shown to increase as a function of gladius length (chapter 2 and 3). Because the samples compared in this study differed in size-structure, inter-sample differences, meant to represent spatial variability in growth, could reflect the effect of size instead. The results were considered size-independent and reflected growth performances during a recent period preceding capture. The implication is that growth conditions varied horizontally along the Gulf Stream and Slope Water frontal system. This variability was minor in 1979, but quite significant in the other years suggesting that (a) growth is not homogeneous among individuals recruiting annually to the feeding grounds off Nova Scotia and (b) isolated samples may not represent annual growth conditions which could limit their use to address recruitment variability. The following analysis is an attempt to explain the main patterns of growth variability in relation to physical processes and the distribution of favourable food environments in Slope Waters. Direct information about previous positions of the analyzed squids was not available. The analysis, therefore, is mostly hypothetical and concerned with major patterns.

Growth during early life is expected when the amount of energy gained in one meal exceeds the energy required to find and obtain the next one. Since young *Illex*

exhibit limited swimming capacity and are energetically expensive (O'Dor et al. 1986), high growth levels probably require food resources to be quite concentrated. The entrainment in the Slope Water during spring (Fig. 1.3) provides access to an environment approximately 4 to 12 times richer in phytoplankton and 3 to 4 times richer in zooplankton than the Gulf Stream (see reviews in Raimont 1980 and Allison and Wishner 1986). Advantageous concentrations of food particles, however, seem 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 (Olson 1986; Arnone et al. 1990; Mann and Lazier 1991; Bakun and Csirke in press). The Gulf Stream and the Slope Water differ sharply in density and relative motion. Their encounter is characterized by a convergent flow which produces, by mixture, a water of intermediate density where food particles tend to accumulate. Zooplankton abundance has been shown to be greater at this front than in the adjacent Gulf Stream and Sargasso Sea (Allison and Wishner 1986). Bakun and Csirke (in press) stressed that the retention of *Illex* paralarvae at this front could particularly enhance growth and survival. Shoreward, at the interface between the Slope Water and the Coastal waters (the shelf/slope front) levels of primary and secondary production are significantly increased and normally exceed those reported for the adjoining Slope and Coastal waters (Fournier 1977; Herman et al. 1981; Allison and Wishner 1986). In this area, the mixed layer is deepened by the action of tidally-generated internal waves and enriched with nutrients from deeper waters (Mann and Lazier 1991). Additional patches of food, in the study area, may further be produced by localized processes of enrichment and particle concentration such as that derived from the flow curvature of meanders (Arnone et al. 1990) and the vertical water mixing of warm-core rings (Olson 1986).

The general pattern, emerging from the analysis of gladius recent growth, suggested that juvenile growth is improved shorewards as squids 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. Two factors may be associated with such contradiction:

- (a) It is possible that diffusion processes related to the meander activity may eject juveniles from the front (Bakun and Csirke in press).
- (b) 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 squids of the 1981 survey near the boundary of the Gulf Stream, (in particular in sample 181) provide some support for a combination of both factors. Firstly, due to the small size of the individuals, paralarval growth was better addressed in these samples than in any other sample considered in this study. Secondly, these samples originated from the easternmost area. Considering that the transport in the Gulf Stream occurs eastward, that would indicate that somehow these squids were retained in the Gulf Stream, near the front. In consequence, unlike juveniles from other surveys, their high recent growth could be explained by favourable food concentrations and higher temperature in the Gulf Stream boundary.

After the entrainment in the Slope Water, growth seemed to be enhanced northeasterly, 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 eastward, 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 northeast (Csanady and Hamilton 1988), probably transporting entrained *Illex* to the shelf/slope front where growth may have been favoured.

Squids with superior 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 the 1982 survey the second highest growth performance was exhibited by squids in sample 182 located away from the shelf/slope front but caught in the vicinity of a ring (Fig. 4.6 and 4.2h). A similar, though less conspicuous, result was observed in sample 489 of the 1989 survey (Fig. 4.8 and 4.2j).

In summary, growth variability observed in juvenile *Illex* can, in many ways, be

associated with the horizontal distribution of food in the Slope Water. Furthermore, processes of surface and subsurface transport may be important factors responsible for the "delivery" of these juveniles to favourable areas. The transport of *Illex* offspring by the Gulf Stream towards the feeding grounds has been compared to a "one-way train" (Bakun and Csirke in press). Individuals may "fall off the train" at any point along this 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 northeastwards towards areas of food concentration on the shelf break. Retained at the Gulf Stream boundary, juveniles may be transported to easterly areas, while benefiting from a favourable concentration of food at the front. In such circumstances, entrainment into the adult habitat may be further advantageous since it would occur in highly productive waters 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 at younger ages in comparison to other southern areas (Morris and Aldrich 1985; Dawe and Beck 1992); a feature that suggests fast growth during early life.

Gulf Stream meanders and eddies vary spatially and temporally (Seaver 1987; Trites and Drinkwater 1984; Myers and Drinkwater 1989; Drinkwater and Trites 1991), and may be related with seasonal and interannual recruitment processes (Dawe and Warren in press; Bakun and Csirke in press). This topic will be addressed in chapter 5.

CHAPTER 5- Seasonal, Interannual and Geographic variability in the juvenile growth of *Illex illecebrosus*.

5.1. Introduction

Typically, the structure of ommastrephid squid populations is complex (Hatanaka et al. 1993). Annual recruits, produced almost continuously by seasonal spawning groups, are spread over a large area by strong geostrophic currents (Hatanaka et al. 1985a; Coelho, 1985) and often form temporally and/or geographically defined subgroups (Coelho and O'Dor 1993; Arkhipkin and Scherbich 1991; Zuev and Nikolsky 1993). Associated with such population diversity and evolving in response to variable environmental conditions, is a variety of intraspecific life history traits that spread the risks of recruitment and may be important components in the mechanisms of population regulation (O'Dor 1992; O'Dor and Coelho 1993; Sinclair 1988). Many of such traits (i.e. sexual maturation, fecundity, mortality) are affected by the animal size and consequently directly related with growth (Calow 1987).

The analysis of size-frequency distributions of various squid populations has provided preliminary evidence for intraspecific growth variation associated with the population structure (Mesnil 1977, Lange and Sissewine 1981, Ehrhardt et al. 1983; Amaratunga 1980). The indirect estimation of growth rates from statoliths and gladii structures has confirmed most previously established patterns and revealed more complex scenarios. Growth has been shown to vary among: (a) geographical populations (Bigelow 1992; Bizikov in press), (b) seasonal spawning groups (Arkhipkin 1990; Arkhipkin and Scherbich 1991; Arkhipkin and Mikheev 1992), (c) monthly cohorts within a seasonal group (Arkhipkin 1990; Rodhouse and Hatfield 1990; Arkhipkin and Scherbich 1991; Dawe and Beck 1992; Uozumi and Shiba 1993), (d) annual generations of the same population (Villanueva 1992; Arkhipkin and Laptikhovsky 1994) and possibly (e) schools (Perez and O'Dor in prep.). In most cases, such variability was attributed to the effect of different temperature regimes and feeding conditions on individual growth.

The population structure of *Illex illecebrosus* distributed along the east coast of North America is mainly defined by seasonal spawning and geography (Coelho and O'Dor 1993, Coelho et al. 1994). Off the coast of Nova Scotia and Newfoundland, the summer and autumn concentrations are composed mainly of winter-spawned individuals. Secondary and tertiary, spring and summer, cohorts predominate in the southern areas along the coast of the United States. In general, the northern population component is the most abundant but also the most variable (O'Dor and Coelho 1993, Coelho et al. 1994). It has been hypothesized that juveniles of this component are exposed to the most favourable growth and survival conditions during spring in the northern areas (O'Dor 1992), but they may also be more susceptible to interannual variations of the environment.

This chapter, examines seasonal and interannual variability in the juvenile growth of *I. illecebrosus* off Nova Scotia, and compares overall growth patterns in this area with those of the southern extremes of *Illex* distribution. The analysis complements the assessment of environmental effects on juvenile growth (see chapter 4) and addresses three main questions: (a) whether *Illex* spring growth is faster in the northern juvenile habitats than in the southern tropical areas of *Illex* distribution; (b) whether overall spring growth conditions off Nova Scotia are more favourable than those encountered by juvenile *Illex* throughout the summer; and (c) whether there is consistent interannual variability in juvenile growth which can be linked to temporal patterns of squid recruitment in the Scotian Shelf. Essentially, this latter analysis intends to compare growth during 1979, a year of high squid abundance, with the subsequent years of fishery collapse.

5.2. Material and Methods

5.2.1. Samples

Most of the material analyzed in this study was described in chapter 4 and included late winter and spring samples of juvenile *I. illecebrosus* collected off the Scotian Shelf between 1979 and 1989. Four additional samples originated from surveys

conducted in June and August 1989 and in February 1985 (Appendix 1). The 1989 summer surveys were part of the 1988-89 program on the distribution of mesopelagic fauna in the Slope and Coastal Waters. Fishing transects and sampling procedures were similar to those described in section 4.2.1. The collections in June (sample 889) and August (sample 989) originated from hauls conducted in the vicinity of the shelf break: Sample 889 was collected in warm Slope Waters, and sample 989 was closely associated with the shelf/slope front. The vertical thermal gradients between 0 and 200 m at the stations 889 and 989, ranged between 15.5-12.5°C and 20.0-8.0°C respectively (Appendix 5). The 1985 survey sampled paralarval and juvenile *Illex* between Cape Hatteras (36°N) and south Florida (25°30'N). Fishing was conducted along five transects across the Gulf-Stream/ Slope-Water frontal system using a Midwater Trawl net (MWT) in oblique hauls from 150m to the surface. Details about sampling procedures and data collection are in Trites and Rowell (1985). The samples analyzed here were collected in transects at 32°30'N (sample 185) and 25°30'N (sample 285) and originated from the shoreward boundary of the Gulf Stream. Gradients of temperature between 0 and 150 m ranged from 14° to 24°C in both locations (Appendix 6). The specimens collected during the surveys in 1985 and summer 1989 were preserved similarly to the rest of the analyzed material, and were also obtained from historical collections in Atlantic Canada (section 4.2.1). The size composition and number of juveniles subsampled for the gladius analysis are indicated in Appendix 1.

The material was grouped according to the sources of intraspecific growth variability addressed. The analysis of seasonal growth included the samples collected in 1989 off the Scotian Shelf and compared growth of squids caught in April (samples 1-789), June (sample 889) and August (sample 989). In the same area, interannual growth variability was assessed by comparing late winter and spring growth in the years: 1979 (samples 1-579), 1981 (samples 1-581), 1982 (samples 1-682), 1988 (samples 1-388) and 1989 (samples 1-789). The analysis of geographic growth variability compared growth of juveniles caught during January 1985 at 32°30'N (sample 185) and 25°30'N (sample 285), with all samples collected in late winter and spring north of 38°N (Appendix 1).

5.2.2. Gladius growth and data analysis

Gladii were extracted from a total of 1393 preserved squids and analyzed according to the methodology described in chapters 2 and 3. Series of growth increments (GInc) were measured in micrometres on the gladius structure and smoothed by a statistical filter. Growth variability was assessed using two different methods: (1) size-specific growth and (2) recent growth.

Size-specific growth was estimated by plotting gladius growth increments (GInc) against the gladius length (GL) at the beginning of each increment formation. Size-specific growth curves were reconstructed by calculating mean GInc per 1 mm GL interval (chapter 3), and used to compare growth conditions of different groups qualitatively. **Recent growth** was defined in this chapter as the total absolute growth (TRG) of the gladius during the last 15 day period. Differences in TRG among juvenile groups were tested by a covariance analysis (ANCOVA) using the "initial" gladius length (GLi), back-calculated to 15 days before capture, as covariate. A test for the interaction between groups and GLi was carried out before each ANCOVA was performed (test of homogeneity of slopes). When the groups were found to be significantly different ($\alpha=0.05$), isolated comparisons were made by Tukey tests applied to the residuals of TRG regressed on GLi.

5.3. Results

5.3.1. Seasonal Variability

Gladius growth increments measured in squids caught in April, June and August 1989 are compared in Fig. 5.1 and Table 5.1. Between 20 and 50 mm GL, GInc of squids caught in June and August were similar, ranging from 0.37 to 0.48 mm in both months. In April, GInc were consistently larger than in the summer samples ranging, in the same growth period, from 0.42 to 0.57 mm.

The initial size (GLi) affected the variability of TRG ($F=462$; $p<0.001$), but did

Table 5.1. Gladius growth increments (in mm) variation of all squid groups analyzed. Mean and standard deviation (SD) were calculated for GInc pooled by 1 mm GL intervals (*n*). Values for years 1979-89 were calculated for all samples collected in late winter-spring pooled by year. 889 and 989 were collected in June and August 1989 respectively; 185 and 285 were collected in January 1985 in 32°30'N and 25°30' respectively.

GL	1979				1981			1982			1988			1989Apr			889Jun			989Aug			185n			285n			
	<i>n</i>	Mean	SD		<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	
10	10	0.40	0.07		240	0.40	0.05	53	0.38	0.05	4	0.49	0.03	17	0.39	0.03	10	0.31	0.03				10	0.29	0.03	15	0.25	0.02	
15	211	0.44	0.04		861	0.47	0.08	511	0.40	0.05	19	0.52	0.07	104	0.38	0.04	26	0.36	0.04				93	0.30	0.03	91	0.28	0.03	
20	243	0.44	0.05		771	0.53	0.09	578	0.42	0.05	65	0.50	0.10	247	0.42	0.04	43	0.36	0.03	8	0.38	0.03	75	0.36	0.03	56	0.31	0.03	
25	122	0.47	0.04		192	0.59	0.08	640	0.47	0.04	62	0.50	0.13	308	0.44	0.05	67	0.40	0.03	68	0.40	0.03	35	0.36	0.03	23	0.36	0.02	
30	53	0.49	0.04		11	0.61	0.06	673	0.50	0.04	32	0.59	0.13	447	0.47	0.06	121	0.40	0.03	193	0.41	0.03	22	0.38	0.02	19	0.38	0.05	
35	97	0.54	0.04					535	0.52	0.05	68	0.67	0.11	530	0.48	0.06	157	0.40	0.04	279	0.42	0.03				5	0.39	0.03	
40	173	0.56	0.06					275	0.54	0.05	96	0.73	0.10	516	0.52	0.07	108	0.43	0.05	239	0.44	0.04							
45	214	0.59	0.07					9	0.58	0.09	100	0.71	0.09	465	0.54	0.06	52	0.46	0.04	94	0.47	0.04							
50	210	0.60	0.06					2	0.72	0.05	56	0.71	0.13	365	0.57	0.06	23	0.49	0.04	5	0.48	0.03							
55	121	0.60	0.06								19	0.73	0.11	323	0.59	0.07	4	0.53	0.02										
60	65	0.62	0.05								6	0.71	0.14	208	0.60	0.09	8	0.50	0.04										
65	17	0.68	0.07											176	0.62	0.09	4	0.56	0.01										
70	5	0.61	0.08											131	0.65	0.07	4	0.65	0.03										
75														87	0.67	0.08													
80														35	0.73	0.08													

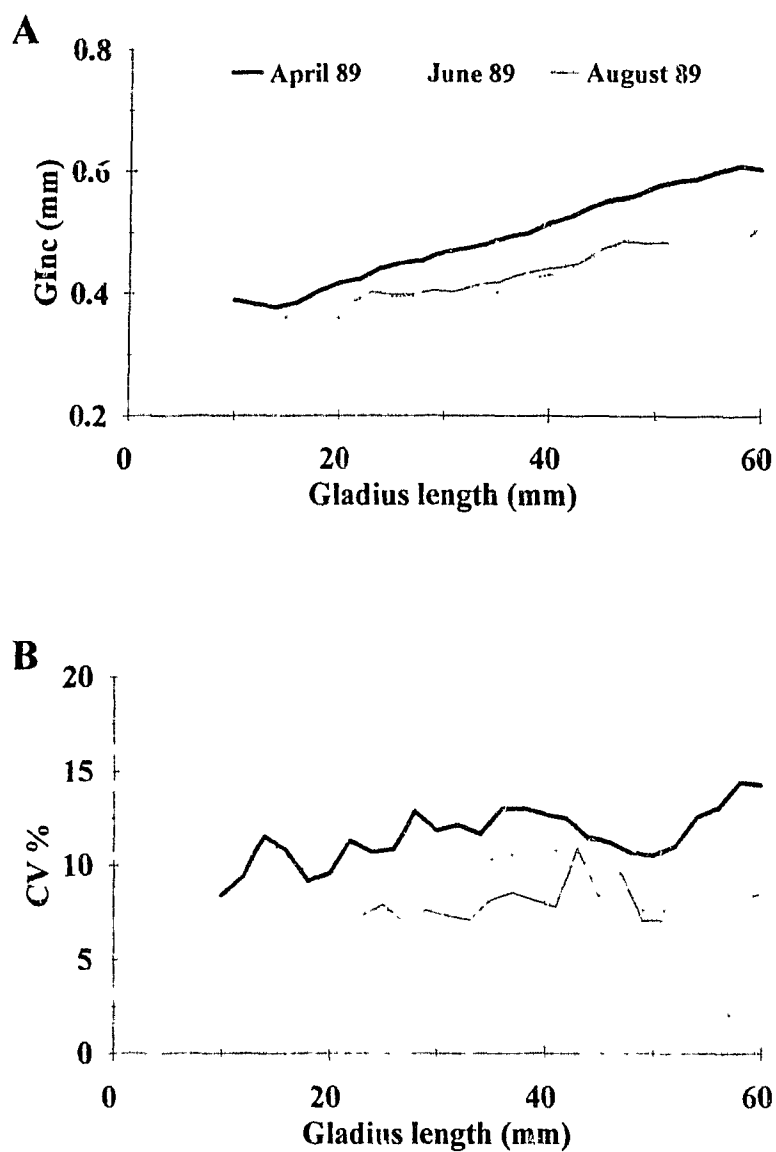


Fig. 5.1. Size-specific variation of gladius growth increments (GInc) measured in squids caught in April, June and August 1989. Means (A) and the coefficient of variation (B) were calculated for GInc pooled by 1 mm GL intervals. Dotted lines indicate a growth period compared in the text.

not interact with months (test for homogeneity of slopes, $F=0.329$, $p=0.72$). Months differed significantly in TRG (ANCOVA, $F=1137$; $p<0.001$; Table 5.2). Isolated comparisons indicated that TRG was significantly superior in April (Tukey test, $p<0.001$; Fig.5.3A), and did not differ between June and August ($p=0.776$).

5.3.2. Interannual variability

Fig. 5.2 and Table 5.1 show the mean size-specific GInc variation in different years off the Scotian Shelf. Squids caught in the 1988 survey exhibited large and extremely variable GInc (Table 5.1; Fig. 5.2). The pattern of size-specific growth also differed considerably from that observed in the other years and its consistency was considered dubious, since the number of squids analyzed in this survey was also limited (section 4.2.2, Appendix 1). Otherwise, GInc measured in squids caught in 1981 were the largest, varying from 0.40 to 0.61 mm between 10 and 30 mm GL (Table 5.1), and diverging sharply from the other years at sizes above 15 mm GL. Between 10 and 20 mm GL, GInc of squids caught in 1979 were higher than those measured in 1989 and 1982. Above 20 mm GL, GInc of 1982 squids approximated those of squids caught in 1979 (Fig. 5.2; Table 5.1).

The analysis of recent growth was carried out excluding the 1988 samples. GLi had a highly significant effect on TRG ($F=992.3$, $p<0.001$) and was shown to interact with years (test for homogeneity of slopes, $F=58.5$, $p<0.001$). Pairwise comparisons between years, indicated that such interaction was mostly driven by particular samples within the 1981 and 1982 surveys (181, 481, 581, 282, 382). When such samples were excluded from the analysis, the GLi \times TRG interaction was eliminated (test for homogeneity of slopes, $F=2.46$; $p=0.062$). TRG differences among years were significant (ANCOVA, $F=26.9$; $p<0.001$): squids caught in 1981 and 1989 exhibited the highest and the lowest TRG respectively (Tukey test, $p<0.001$); squids of years 1979 and 1982 did not differ significantly in TGR ($p=0.955$; Fig.5.3B). Such results were considered consistent despite the selective removal of the previously mentioned samples. With

Table 5.2. Seasonal, interannual and geographic comparisons of the total recent growth (TRG) measured on the gladius of juvenile *Illex illecebrosus* (ANCOVA). The grouping factors were SEASON (April, June and August 1989), YEAR (1979, 1981, 1982, 1988, 1989) and AREA (north of 39°N, 32°30'N and 25°30'N). The gladius length at the beginning of the measured recent growth increment (GLi) was the covariate. The analysis was preceded by a test for homogeneity of slopes (see section 5.3). Degrees of freedom (df), mean squares (MS) and *F*-ratios, are indicated. Asterisks indicate *p*-values below 0.001.

Source	df	MS	<i>F</i>
<u>Seasonal</u>			
GLi	1	474.81	856.68*
SEASON	2	63.04	113.68*
Error	412	0.54	
<u>Interannual</u>			
GLi	1	712.65	1463.27*
YEAR	3	13.10	26.90*
Error	732	0.49	
<u>Geographic</u>			
GLi	1	296.06	1121.37*
AREA	2	92.60	350.73*
Error	449	0.26	

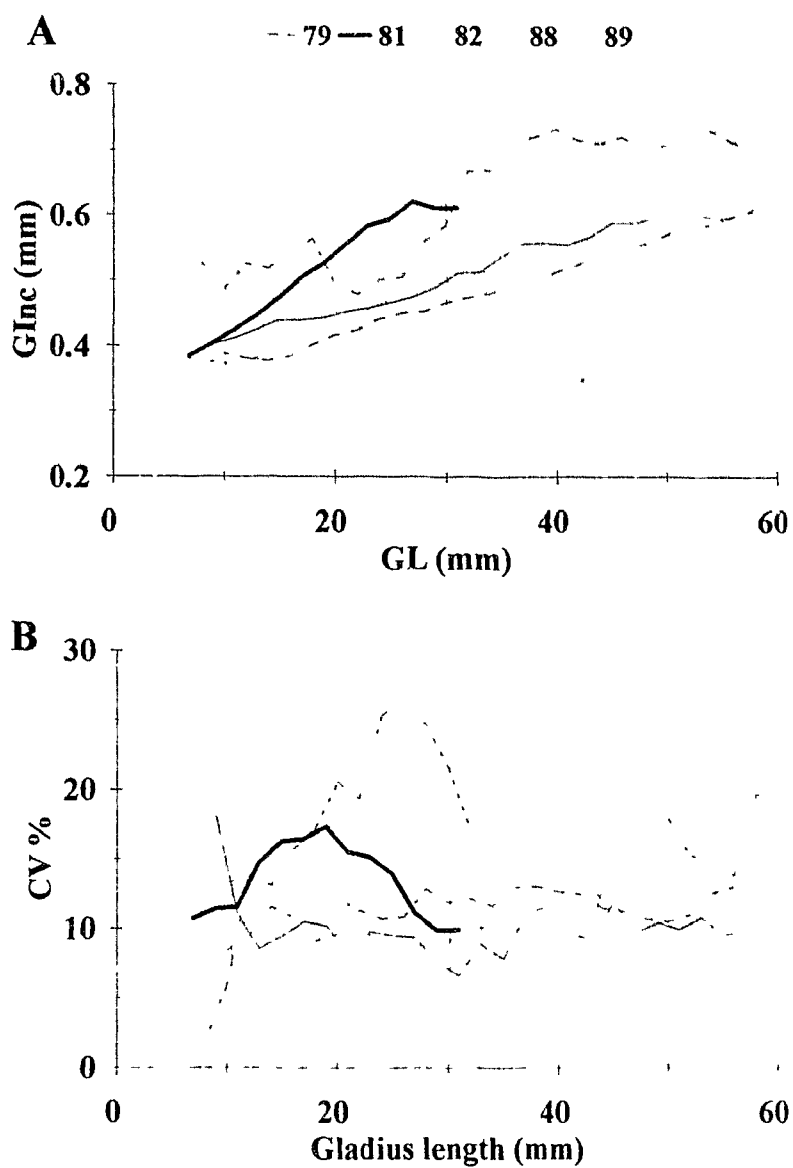


Fig.5.2. Size-specific variation of gladius growth increments (GInc) measured in squids caught in late summer-spring of 1979, 1981, 1982, 1988 and 1989. Means (A) and the coefficient of variation (B) were calculated for GInc pooled by 1 mm GL intervals. Dotted lines indicate a growth period compared in the text.

exception of sample 181, all excluded samples did not deviate sharply (less than 50% of one standard deviation) from their survey's mean $G_{inc} \times GL_i$ residual (section 4.3.2, Fig. 4.2G-H). Sample 181 exhibited a considerably superior growth in the 1981 survey which, *a priori*, would agree with the pattern indicated by the present analysis (Fig. 4.2G; 5.3B).

5.3.4. Geographic variability

Gladius growth increments of squids caught in January south of Cape Hatteras were the lowest among all the analyzed material (Fig 5.4) varying, between 10 and 30mm GL, on average, from approximately 0.26 to 0.38 mm (Table 5.1). Below 30 mm GL, G_{inc} in sample 185 (32°30'N) was larger than in the sample 285 (25°30'N; Fig 5.4).

The recent growth analysis initially compared samples collected in 1985 and the northern samples pooled (1979, 1981, 1982 and 1989). GL_i affected TGR variability ($F=570.8$, $p<0.001$) and interacted significantly with the areas (test for homogeneity of slopes, $F=86.0$, $p<0.001$). Isolated comparisons conducted between 1985 and each of the northern surveys, indicated that 1982 was the only year in which the $GL_i \times Area$ interaction was not significant (homogeneous slopes, $F=1.435$, $p=0.232$). Therefore the ANCOVA, testing for differences in TRG between northern and southern areas, included samples from 1982 and 1985 respectively. TRG was lowest in 285, intermediate in 185 and highest in the northern samples in 1982 ($F=679.1$, $p<0.001$; Tab. 5.2; Fig. 5.3C).

5.4. Discussion

It has been suggested that the gladius accretive growth may be sensitive to external and internal factors affecting somatic growth. In chapter 3, for example, temperature variation and feeding events may have been detected in the gladius growth series. Field studies with *Sthenoteuthis pteropus*, *Kondakovia longimana* and *Illex illecebrosus* have also suggested that sexual maturation, lunar cycles, availability of food and the effects of the Antarctic winter were associated with growth patterns identified on

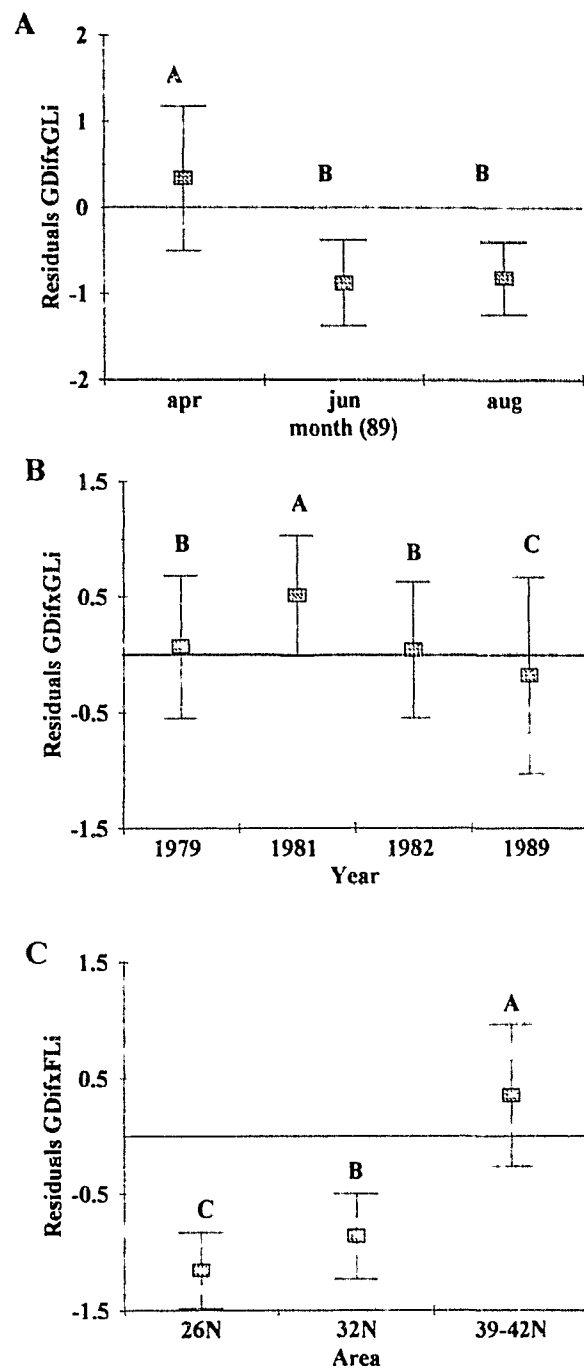


Fig. 5.3. Mean residuals of the total recent growth analysis. Residuals were calculated from the regressions of TRG on GLi. Capital letters on top of bars and symbols indicate the result of the Tukey tests: classes labelled with different letters are significantly different ($p < 0.05$). A. Seasonal growth analysis; B. Interannual growth analysis; C. Geographic growth analysis. The area north of 39°N correspond to samples of 1982.

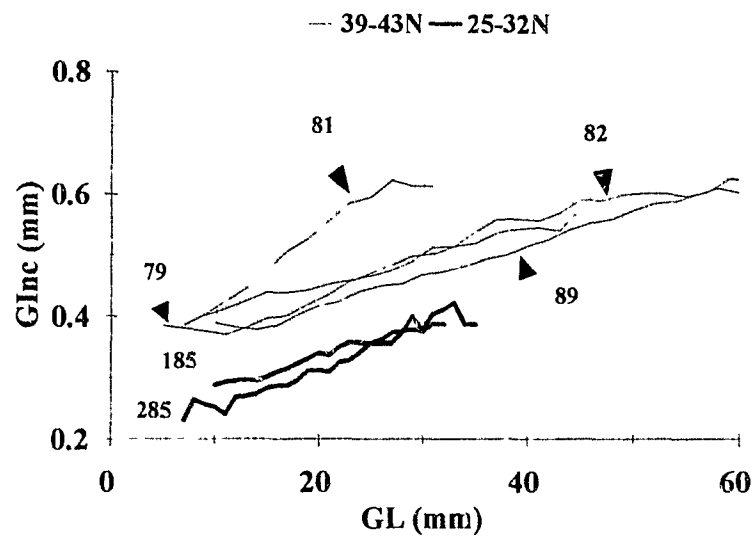


Fig.5.4. Size-specific variation of gladius growth increments (GInc) measured in squids caught in January 1985 between Cape Hatteras and Florida (185 and 285; thick lines) in comparison with results showed for the northern areas (also in Fig. 5.2, light lines). Means (A) and the coefficient of variation (B) were calculated for GInc pooled by 1 mm GL intervals. Dotted line indicate a growth period compared in the text.

the gladius structure (Bizikov 1991; Bizikov in press; Perez and O'Dor in prep). Despite the preliminary nature of these observations, the applicability of gladius-reconstructed individual growth on the assessment of intraspecific sources of growth variability seems promising. A first attempt was presented by Bizikov (in press) who detected population differences in the gladius growth of the ommastrephid *Sthenoteuthis pteropus*. The present study, the second of its kind, revealed geographic, seasonal and possibly interannual patterns in the gladius-reconstructed juvenile growth of *Illex illecebrosus*. The interpretation of these patterns mostly deals with (a) predominant factors affecting growth ("causes" of growth) and (b) the dynamics of the population size-structure on the feeding grounds ("consequences" of growth).

Seasonal growth variability

Gladius growth increment variation in 1989, revealed that juvenile growth was enhanced in spring and declined during the summer months. This pattern was consistent with cycles of biological production in the slope water, but inversely related with seasonal temperature fluctuations. Primary and secondary production peak annually between March and May, when temperatures are relatively low in the Slope Water. Throughout the summer, as temperatures increase, production declines (Zheng et al. 1984; Judkins et al. 1980; Kuring et al. 1990; Allison and Wishner 1986 and Raymont 1980 for review). Increased feeding rates, utilizing higher concentrations of food during spring, may have compensated for lower temperatures and therefore enhanced juvenile growth (see chapter 3). Statolith ageing of immature *Illex* off Newfoundland indicated that squids hatched from March to May were progressively larger at the same ages, suggesting that growth increased throughout summer and autumn (Dawe and Beck 1992). While these results do not seem to support the interpretation provided by gladius growth variations, it should be noted that in the study by Dawe and Beck (1992): (a) size-at-age variability was high; (b) smallest individuals aged were around 150-160mm in mantle length, thus not necessarily revealing juvenile growth, and (c) the production peak in that area (i.e. the Grand Banks and further north) seems to occur later than that on the Scotian Shelf (Robinson et al.

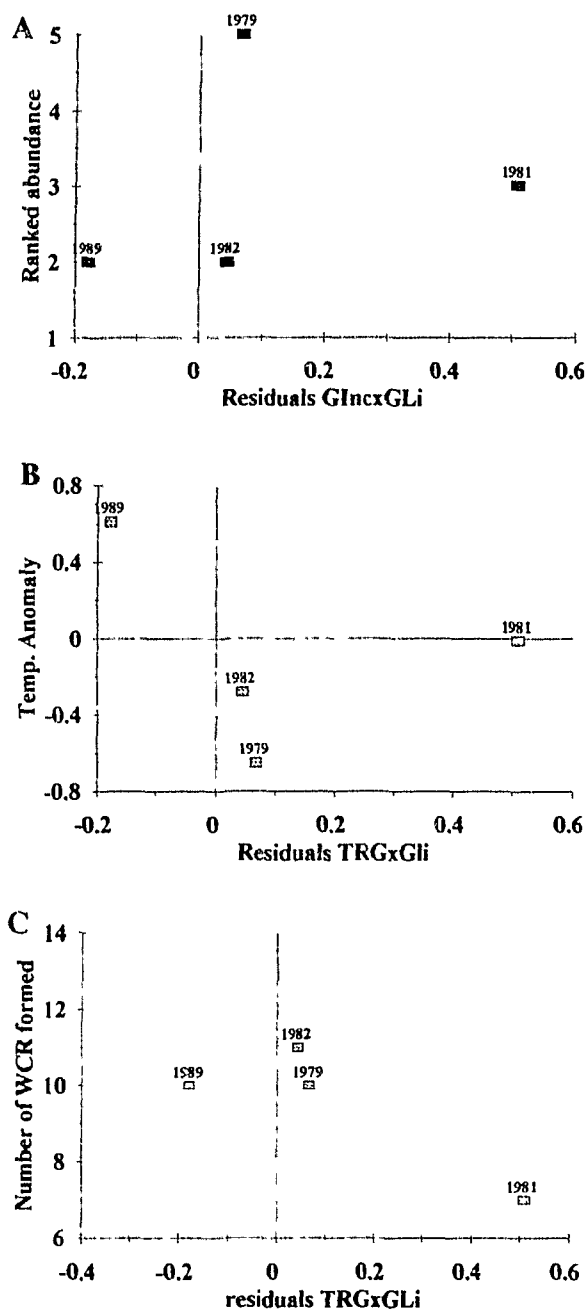


Fig. 5.5. Relationships between interannual patterns of TRG (residuals TRGxGLi) and (A) *I. illecebrosus* ranked abundances off Nova Scotia and Newfoundland; (B) Temperature anomalies in the eastern Slope Water; (c) Number of warm-core rings (WCR) formed east of 60°W. Sources: Dawe and Warren in press; Trites and Drinkwater 1984; Drinkwater and Trites 1991).

1975; Prasad and Haedrich 1993).

Evidence for a positive effect of temperature on seasonal growth rates in squid populations, was more substantial in ageing studies conducted on *Illex argentinus* in the Southwestern Atlantic. In that area, it has been shown that juveniles tend to grow faster during the warmer austral summer and autumn than during the colder austral winter and spring (Arkhipkin and Scherbich 1990; Rodhouse and Hatfield 1990; Arkhipkin and Laptikhovsky 1994). However, possible differences in the northern and southern Atlantic ecosystems may account for such a discrepancy. In the Patagonian shelf, seasonal wind-induced upwellings do not seem to occur (Bakun and Csirke in press). Biological production is sustained throughout spring and summer at the shelf break (main habitat of juvenile *Illex*), probably as a result of tidal fronts and other physical mechanisms of local enrichment (i.e. upwelling in frontal eddies, interaction between internal waves and the shelf break; Podestá 1990). Although comparable information on biological production is not available, it seems that food availability during spring and summer in the *I. argentinus* juvenile habitat is more stable; in which case the effect of temperature fluctuations on growth could predominate.

Interannual growth variability

Interannual growth variability during the feeding period on the shelf, has been detected from changes in mantle length frequency-distributions (*I. illecebrosus*; Amaratunga 1980) and from statolith-determined size-at-age data (*I. argentinus*; Arkhipkin and Laptikhovsky 1994; and *Todarodes angolensis*; Villanueva 1992). In none of these studies, however, was there indication whether growth also varied during the juvenile phase (i.e. variation in size-at-age of recruits). In juvenile *I. illecebrosus*, the evidence for interannual variation in the juvenile gladius growth is also sketchy and probably masked by other sources of intraspecific growth variability (i.e. seasonal, spatial). In particular, the 1981 samples, exhibiting the fastest growth, originated from a distinct area and oceanographic conditions (see section 4.3.2) and may not have been comparable to those

from other years.

Attempts to relate growth patterns with annual levels of squid abundance (Dawe and Warren in press) and major environmental fluctuations (Drinkwater and Trites 1991) have produced mostly inconclusive results (Fig. 5.5). Some inferences, however, can be made from the superior growth observed during 1981. As hypothesized in chapter 4, the fast growth exhibited by these juveniles could have been related to an extended retention at the boundary of the Gulf Stream, where food particles are concentrated (Bakun and Csirke in press). Such a process would largely depend on the integrity of the front, normally disrupted by meanders, frontal eddies and rings (Rowell and Trites 1985; Bakun and Csirke op cit.). Interestingly enough, numbers of warm-core rings were remarkably low in 1981 (Fig. 5.5) which might have resulted in: (a) paralarval retention at the Gulf Stream boundary; (b) transport to easterly areas and (c) enhanced growth (Trites and Drinkwater 1984). Growth in 1979, a year of high *Illex* abundance, was found to be fast during the feeding period on the shelf (Amaratunga 1980). During the juvenile phase, however, as shown by the size of recruits at the beginning of that season and by their gladius growth increments, growth was not exceptional. The lowest growth observed in 1989, was probably the strongest indication of interannual variability. Positive temperature anomalies (0.61°C) were reported for the eastern Slope Water during that year (Drinkwater and Trites 1991).

A potential powerful alternate approach to address interannual changes in growth with the data presented here, would derive from the analysis of backcalculated gladius length composition of squid samples at fixed "dates" across years. In *Illex* populations, however, this approach has some important limitations. As shown by previous studies, the size composition of juvenile *Illex* on the Slope Water may vary greatly (Fedulov and Froerman 1980; Froerman et al. 1981; Amaratunga 1981; Dawe et al. 1982; Dawe and Beck 1985a and b; Rowell et al. 1985; Hatanaka et al. 1985; Rowell and Trites 1985). The implication is that several population components may overlap in the area either due to continuous spawning or to differential time and place of entrainment in the Slope Water (Rowell and Trites 1985). These results have also been supported by age studies using the statolith growth (Arkhipkin and Scherbich 1991, Dawe and Beck 1992). Thus,

without a clear distinction of population components, e.g. without information on age and hatching dates of the juveniles analyzed, it is difficult to separate interannual influences on growth from those derived from the mixing of individuals with different chronologies. Size-at-date might be a more powerful indicator of recruitment success, but only works if the gladius technique is combined with statolith-determined age estimations. Although promising, this approach can only be applied in samples fixed to preserve statoliths.

Geographic growth variability

Gladius growth increments were remarkably smaller in the southernmost areas of *Illex* distribution. The interpretation of this pattern, however, is difficult. The area comprises the suspected common spawning grounds of *I. illecebrosus* (Trites 1983; Rowell and Trites 1985), where adult concentrations occur throughout the year mainly over the shelf break (Ratjhen 1981; Whitaker 1980). A local population component is believed to exist (O'Dor 1992; O'Dor and Coelho 1993), but biological information is limited. Rowell and Trites (1985) and Goldman and McGowan (1991) reported the presence of paralarval and juvenile *Illex* between Florida and Cape Hatteras. It was suggested that, despite the potential for northward transport by the Gulf Stream, frontal eddies and warm-core rings may promote early entrainment in the Slope and coastal waters. Transported southward by these waters, young *Illex* could again encounter the northward flowing Gulf Stream and be carried back north. By then, they could be large enough to remain actively in the southern areas, and recruit to the local population. Several fish and crustacean populations in the slope areas are retained by the same mechanism (Kelly et al. 1982; Cowen et al. 1993).

O'Dor and Coelho (1993) proposed that tropical components of *Illex* populations were formed by individuals that remained close to the spawning grounds ("stays-at-home") and that, induced by high temperatures and food limitation, these would mature at small sizes. Whether the theory involves restricted juvenile growth, is unclear. In fact, interspecific growth comparisons tend to confirm that tropical species are generally

smaller but actually grow faster than temperate species; a feature attributed to higher environmental temperatures (Jackson and Choat 1992). The environment where the 1985 juveniles were caught is indeed, considerably warmer than at the frontal zone off the Scotian Shelf. Consequently, the distinctive slow growth in the 1985 samples is not consistent with a positive effect of temperature (Forsythe and Van Heukelem 1987), but may reflect limiting food resources and/or genotypic variability (O'Dor 1992, Coelho et al. 1994). General patterns of phytoplankton and zooplankton distribution in the Northwest Atlantic predict lower levels of food abundance near the tropical areas (see Raimont 1980 and 1982 for reviews). Biological production, however, is enhanced at the shelf-break as result of local upwelling induced by frontal eddies and meanders of the Gulf Stream (Yoder 1985; Paffenhöfer 1985). Although paralarval and juvenile *Illex* seem to take advantage of these patches of food (Rowell and Trites 1985) high growth may not be sustained due to their sporadic nature (Yoder 1985; Paffenhöfer 1985). A similar conclusion supported the fact that in spite of the high abundance of fish larvae and the adequate food supply, these sub-tropical seas (the South Atlantic Bight) did not sustain large fish stocks (Paffenhöfer 1985).

An additional source of complexity is the presence in the area of another species, *I. coindetti* and, perhaps a hybrid with *I. illecebrosus*, *I. oxygonius* (Roper et al. 1983); the former is most common in the Gulf of México (Voss and Brackoniecki 1985). Since they are all very similar at early stages, the possibility of a mixture in the samples exist. Although such an artifact could affect the interpretation based on *I. illecebrosus* population structure, inferences about the contrasting effects of temperature and food conditions in growth should still be valid interspecifically.

General conclusions

Combined with small-scale growth variability shown in chapter 4, the present results confirm the potential of the gladius technique to address intraspecific sources of growth variability. In addition, since the sensitivity of gladius growth increments seems also to be high, inconclusive results may arise if the sources of growth variation assessed

are not properly isolated (e.g. in the interannual analysis).

The results supported the general following theory: juvenile *I. illecebrosus* seem to find superior growth conditions in the northern areas during spring. A relationship between interannual growth variability and squid recruitment, however, could not be established at this point; annual growth patterns were mainly affected by the spatial and seasonal patchiness of the environment (see chapter 4) and did not represent adequately the overall annual growth conditions off Nova Scotia.

As discussed in previous chapters, gladius growth patterns consistently contradicted the positive effect of temperature on growth. Although more comparative studies are needed, it is clear that the relationship of growth to food and temperature is complex and not well understood. Emerging field data on seasonal growth rates, have generally supported the positive effect of temperature (Arkhipkin and Scherbich 1990; Rodhouse and Hatfield 1990; Arkhipkin and Laptikhovsky 1994). Interannual growth differences, however, have indicated superior growth in cold years (Villanueva 1992; Arkhipkin and Laptikhovsky 1994). It appears that the effects of these factors vary according to the characteristics of the oceanographic systems to which the squid populations are adapted. In areas where biological production is substantially enhanced by the upwelling of cold, nutrient-rich waters, the effect of temperature is masked; e.g. *Todarodes angolensis* in the Benguela upwelling system grows faster in colder and more productive years (Villanueva 1992) and *I. illecebrosus* off Nova Scotia grows faster during colder and more productive spring months. In areas where food is more evenly (temporally or spatially) distributed, the effect of temperature may prevail.

CHAPTER 6 - General discussion and conclusions

This thesis investigated the effects of the environment and of life history events on the juvenile growth dynamics of the short-finned squid *Illex illecebrosus*. The main conclusions are:

- a.) The form and variability of *Illex* growth is associated with size-specific events such as ecological transitions and sexual differentiation. The juvenile/offshore growth phase is exponential. A change to linear growth occurs during the adult/onshore life-style (GL > 80-90 mm). During the juvenile phase, a major change in body shape and a separation between two size-specific growth phases are related with the transition from the macroplanktonic to micronektonic habitats (30-40 mm GL). Sexual growth differences occur even among subadults (GL > 120 mm), prior to the onset of maturation.
- b.) Juvenile growth condition is affected by important gradients of temperature and food availability across the Gulf Stream/ Slope Water frontal system. Young *Illex* are energetically expensive and food limited in warm Gulf Stream waters (their hatching environment). Growth conditions improve as they move onshore where colder and food-enriched environments are reached. In these conditions metabolic costs decrease and more food becomes available.
- c.) In the Slope Water off the Scotian Shelf, the oceanographic structure and the associated areas of food concentration partially explain the spatial variability of growth condition of juvenile *Illex*. Growth is enhanced shoreward and particularly in proximity to the shelf/slope front. The processes of transport in the Gulf Stream and Slope Water may play an important role in providing the access to and retention of individuals in these favourable areas.
- d.) Growth conditions of juveniles entrained in the Slope Water off Nova Scotia vary seasonally in association with cycles of biological production. The increased spring production favours juvenile growth.
- e.) A relationship between juvenile growth, interannual fluctuations of the Slope Water

environment and the dynamics of *Illex* recruitment is complex and requires further analysis of related variables.

- f.) Juvenile growth of *Illex sp.* is markedly slower in tropical waters. This result contradicts the general notion that growth in tropical cephalopods is faster due to the positive effect of high temperatures.

The overall implications of the patterns described above on the population biology of *I. illecebrosus*, support general theories (O'Dor 1992; O'Dor and Coelho 1993; Coelho and O'Dor 1993, Coelho et al. 1994). Juveniles are exposed spatially (both in the local and geographic sense), seasonally and interannually to a variety of environments. Growth patterns, as reconstructed from the gladius structure, could be considered as a direct response to such environmental variability. The major winter-spawned population component, reaches the feeding grounds off Nova Scotia and Newfoundland in the spring and encounters the most favourable environment. Southern components, retained in the tropical areas surrounding the spawning grounds, face growth-limited conditions.

The access to food seems to be a major factor shaping the early life history of *I. illecebrosus*. Onshore migrations are driven by the elevated feeding requirements and involve physiological adaptations to compensate for decreasing temperatures. The individual "success" in terms of growth and survival, may depend on the access to concentrated patches of food which in turn will be determined by timing and the transport dynamics of the main water masses. Such access may be particularly critical during important life-style transitions.

Significant variability in juvenile growth is associated with the homogeneity of squid distribution and the heterogeneity of food distribution in the juvenile habitat. In consequence, the probability that juvenile growth estimated from individuals in the Slope Water will reflect annual survival conditions and predict overall squid productivity is low. Since growth within samples was typically homogeneous, one approach to improve correlations would be to increase the number of samples analyzed, while limiting the number of individuals. Alternatively, future studies could compare gladius growth patterns

with temporal and/or spatial distribution of food and the associated oceanographic processes. The interannual variation of the processes that produce the food patchiness and control the access of juveniles to favourable patches may play an important role in recruitment variability. A remarkable tool for this purpose is the interpretation of the ocean colour, as derived from satellite imagery. Although this approach was recognized too late for inclusion in this thesis, its potential is indicated in Fig. 6.1, where the average growth of two samples collected during the 1979 survey parallels the increasing concentration of pigments across the Slope Water and shelf/slope front (see also Fig. 4.4).

Regarding general aspects of squid's early life ecology, the results of this thesis also allowed the evaluation of some previously hypothesized processes and the formulation of new questions for investigation. A brief discussion of such questions and of the potential of the gladius method to approach them is given below.

Form of juvenile growth

Important intraspecific size-selective pressures in the adult habitat may occur in association with the formation of schools, hierarchical access to food and cannibalistic behaviour (Hirtle et al. 1981). In consequence, juvenile *Illex* appear to invest highly in growth in order to attain minimum subadult sizes. This phase, however, is extended, lasting nearly one third of the animal's life span. This feature, also reported for several cephalopods in the field and in captivity (see Forsythe and Van Heukelem 1987 and Jackson in press for reviews), contradicts the predicted adaptative value of fast growth through the vulnerable early life, often characterized in the growth mode of fish larva (Zweifel and Larkin 1981; Calow 1987; Jackson in press). Why can squids afford to start smaller and to remain small for such a relatively large part of their life? A comparative analysis with the ecological pressures faced by larval fish, for example, may provide some hypothetical explanations.

Firstly, fish swimming activity becomes less energetically demanding as the animal grows. On the contrary, the jet-propelled squid's locomotion, is proportionally less

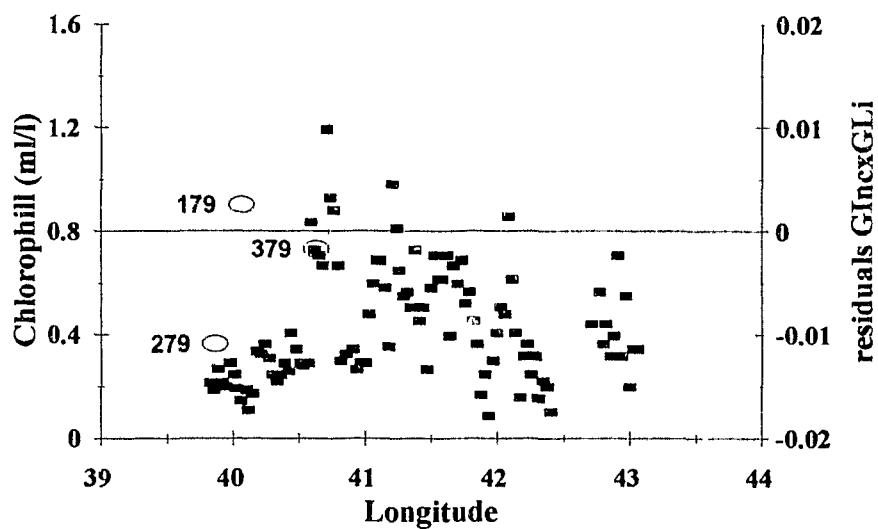


Figure 6.1. Mean growth residuals of squids caught in the 1979 survey in relation to the distribution of chlorophyll. Pigment concentration along a N-S transect (64° W, see Fig. 4.4) was estimated from the analysis of an image obtained April 4, 1979 by Coastal Zone Color Scanner (CZCS, Nimbus-7). Sample 179 was located west of the transect.

expensive at small body sizes (O'Dor and Webber 1986). Thus small squid may actually be less energetically constrained than small fish. Secondly, the effect of predation, which is an important source of negative size-selection in fish (Hunter 1981), may be less critical for young squid. As previously discussed, paralarvae and juveniles are relatively scarce, fast, cryptic and "aware" of the surrounding environment; they are also provided with defense mechanisms such as the ink jet (Boletzky 1987). Finally, a squid can apprehend prey at least as large as its own body (Vecchione 1991) allowing it to feed in the same part of the prey size spectrum as fish larvae at a much smaller size. In addition, the availability of food items, which is normally proportional to the bite size in fish, would increase less significantly as a function of squid size. It is important to note, however, that ecological transitions associated with squid size increase do seem to affect growth (chapter 3). This effect may not necessarily be derived from different prey sizes but from different prey types instead (Vecchione 1987). These questions can be elucidated in the future, as juvenile growth trajectories of more species are described either by the gladius method or by statolith size-at-age data (Balch et al. 1988; Bigelow 1992; Bigelow and Landgraf 1993), and compared to prey spectra (Vecchione 1991; Vidal 1994b).

The effects of temperature and food on growth

Throughout this thesis, growth variability was largely related to food availability. In no circumstance, however, was the positive effect of temperature found to prevail. *Illex* seems to find better growth conditions in colder and more productive geographic areas, water masses and seasons. This pattern is predicted by poekilotherm bioenergetic models (Brett 1979; O'Dor and Wells 1987; Brandt 1993) and has been demonstrated empirically for squid and fish (Brett et al. 1969; Hawkins et al. 1985; Forsythe and Van Heukelem 1987). The positive effect of temperature is most noticeable if food is abundant. In restricted food conditions, growth tends to be enhanced in colder temperatures because metabolic costs are reduced and a greater proportion of the assimilated energy is available for growth (Brett 1979). Thus if food limits paralarval growth, the transition from warm Gulf Stream waters to cold Slope Waters would be favourable (Brandt 1993). Considering

that the Slope Waters are more productive and may provide a considerably denser prey field, the advantage is clear. The same interpretation may apply to patterns of growth variation in response to geographical and seasonal gradients of temperature and food abundance. The possible effect of the vertical distribution of food and temperature on growth may be critical to squids, but was outside the scope of the thesis. Squids, from very young stages, undergo pronounced vertical migrations (Vecchione 1987) and may take advantage of food and thermal structure to be more economical and enhance growth (McLaren 1963). In such circumstances, the juvenile growth efficiency assessed (chapter 3) would be somewhat underestimated. The gladius growth data presented in this thesis will be useful in the future to address this mechanism.

Methodology

The methodology was a crucial part of this thesis. The gladius plate of *I. illecebrosus* did not provide an estimate of age; yet, its potential for growth history reconstruction, was remarkable. Patterns of growth reconstructed in squid samples were generally consistent and provided coherent ecological interpretations. In captive animals, preliminary evidence for individual responses to temperature fluctuations and feeding events was presented. The approach provides the opportunity to address population ecology historically and also establishes a new use for extant museum collections. More comprehensive studies are expected if applications of the gladius technique are coupled with age estimates provided by the statoliths.

An effective application of the gladius technique in ecological studies, however, still requires many technical and methodological adjustments to be made. Errors in growth mark interpretation need to be estimated. Experimental work is needed, in particular to fully validate the 1 mark: 1 day hypothesis and to evaluate the feeding/growth lag and the sensitivity of gladius growth to biotic and abiotic factors. The use of chemical or mechanical methods for marking the gladius structure may prove useful for such purposes. Although this experimental approach is difficult in fast-swimming offshore ommastrephids, it may be achieved successfully in more manageable loliginid squids.

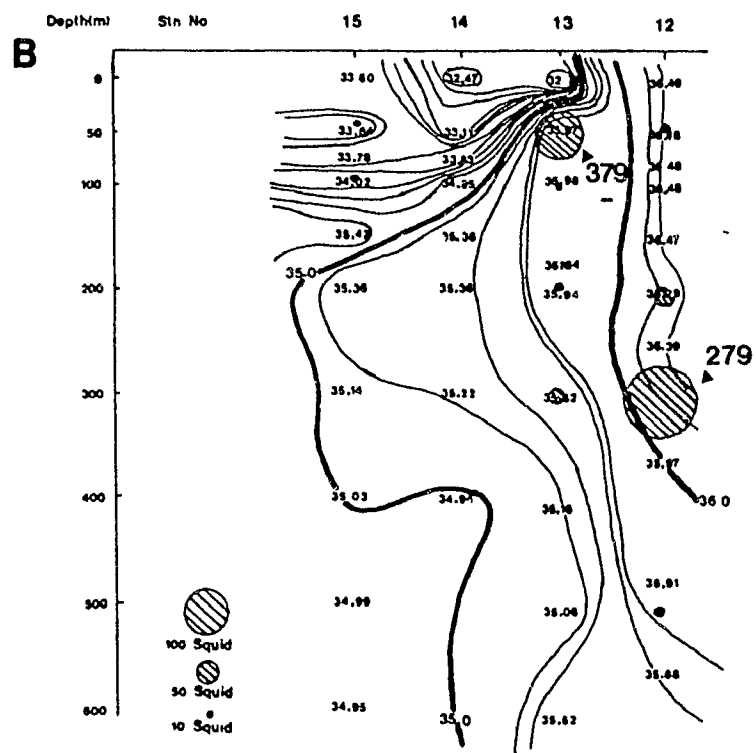
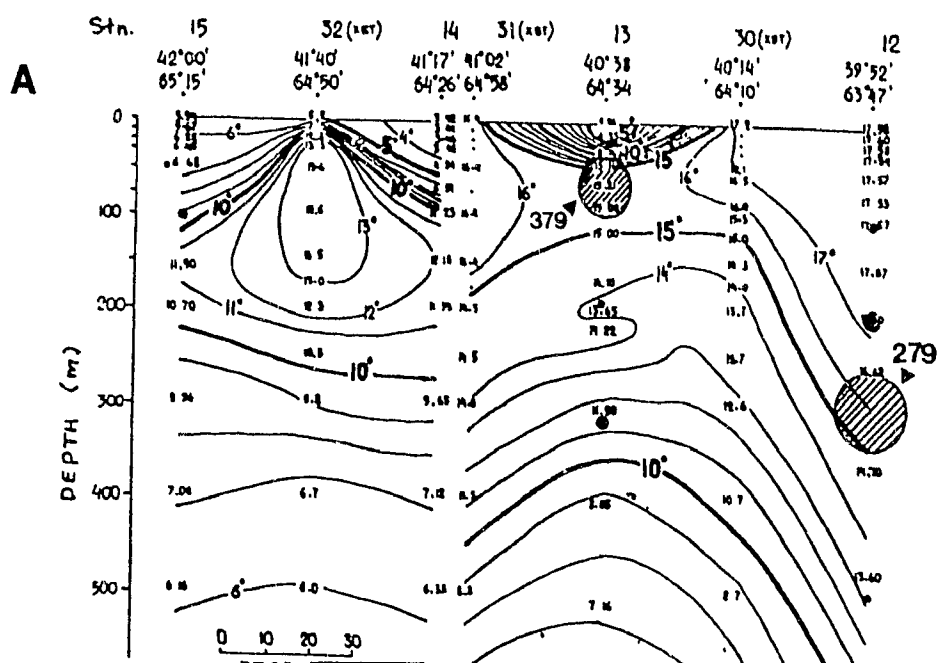
APPENDIX 1

Summary of the samples of the short-finned squid, *Illex illecebrosus*, analyzed in this study. Depth of the trawl is expressed in metres. Salinity at surface is expressed in ppt. and temperature, *in situ* (net) and at the surface, is expressed in degrees celsius. In the 1988-1989 and 1985 surveys, the net temperature corresponds to the value measured at 200 and 150 m depth respectively. n.sq., total number of squids caught; ssamp., subsample taken for gladius analysis. Mean, standard deviation (SD); maximum (max) and minimum (min) gladius length are indicated in millimetres. The net types are: EMT, Engler Midwater Trawl; 510PT, 510 Pelagic Trawl; IYGPT, International Young Gadoid Pelagic Trawl; BOT, Bottom Otter Trawl; YANKEE, Yankee-36 Trawl.

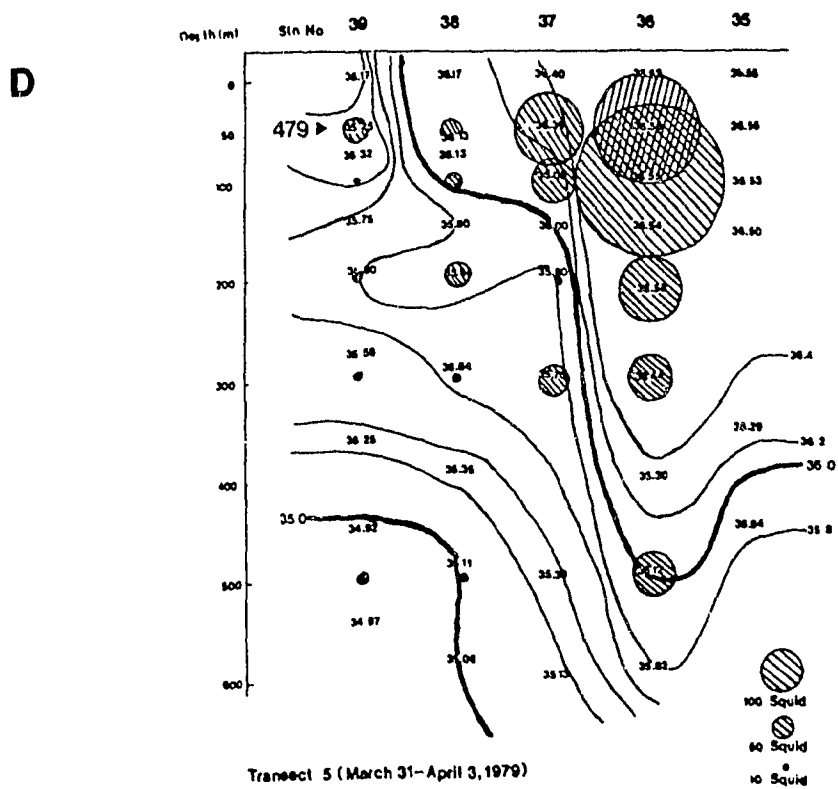
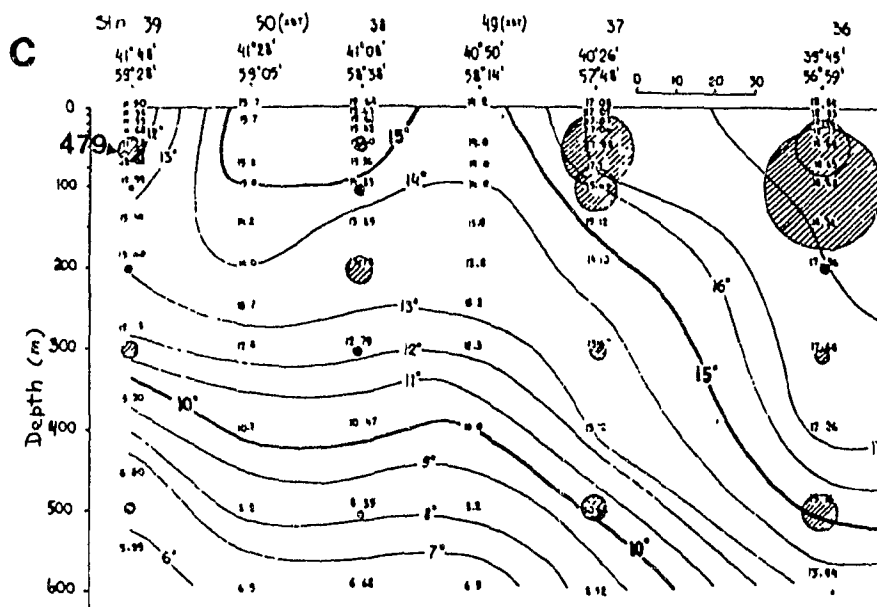
Year	Vessel	Cruise	duration	Sample	Station	Lat. N	Long. W	Date	Depth	Temperature		Sal.	n.sq	ssamp	Gladius Length				net
										net	surf.	surf.			med	SD	min	max	
1979	Belogorsky	7902	Mar. 7-26	179	1	40.04	65.38	Mar. 10	50	15.0	-	-	31	-	26.0	3.81	18.7	36.6	EMT
				279	5-3	39.52	63.47	Mar. 16	300	16.6	17.6	36.49	18	-	27.9	3.39	20.0	36.2	EMT
				379	7-1	40.38	64.34	Mar. 17	50	15.2	4.3	32.70	20	-	20.9	1.55	17.5	24.3	EMT
	Belogorsky	7903	Mar.26 - Apr.4	479	34-1	41.48	59.28	Apr. 03	50	11.8	11.5	35.25	31	-	61.2	5.59	52.8	73.5	EMT
				579	39-2	41.01	56.48	Apr. 05	200	13.8	13.8	35.84	49	-	52.4	5.92	40.3	66.1	EMT
1981	Gadus Atlantica		Feb.20 - Mar.11	181	15	39.12	53.00	Mar. 03	100	15.1	15.0	-	223	99	26.5	1.93	22.5	33.4	EMT
				281	9	40.38	56.01	Feb. 25	100	15.8	18.0	-	160	32	23.7	1.90	19.1	27.1	EMT
				381	8	40.42	56.06	Feb. 24	1000	9.0	18.0	-	170	33	20.4	1.92	16.8	24.8	EMT
				481	8	40.41	56.00	Feb. 25	300	13.2	18.0	-	151	39	22.1	2.10	17.2	26.1	EMT
				581	12	38.23	56.00	Feb. 27	100	19.1	18.0	-	232	102	18.9	2.92	14.2	29.6	EMT
1982	Lady Hammond	H070	Feb. 2 - 25	182	27-2	39.54	61.05	Feb. 17	100	15.5	14.8	35.84	67	-	24.2	4.53	13.5	34.0	510 PT
				282	57-1	40.58	60.04	Feb. 23	50	11.4	14.4	-	37	-	25.4	3.28	16.2	33.9	510 PT
				382	13-1	39.00	62.02	Feb. 07	50	15.2	15.0	35.70	72	-	22.0	5.40	13.8	38.0	510 PT
				482	59-4	42.02	60.00	Feb. 23	500	13.0	10.3	-	40	-	42.2	2.39	36.9	50.3	510 PT
				582	37-1	39.01	60.58	Feb. 18	50	14.0	13.4	35.74	53	-	38.8	3.55	29.7	45.2	510 PT
				682	46-2	39.33	60.08	Feb. 21	100	13.2	13.9	35.70	194	67	38.2	3.21	29.7	46.8	510 PT
1985	Needler	8501	Jan. 12-26	185	45-2	31.15	79.40	Jan. 12	0-150	16.0	23.0	-	214	61	16.8	4.50	9.7	26.2	MWT
				285	96-2	25.30	80.10	Jan. 21	0-150	14.0	23.0	-	190	60	17.5	7.75	7.8	57.4	MWT
1988	Needler	NO96	Feb. 15-26	188	7	41.21	59.00	Feb. 18	50-200	12.4	14.4	35.73	25	36	27.3	3.79	17.5	32.7	IYGPT
					8	41.09	59.01	Feb. 18	50-200	14.8	13.1	35.74	7						IYGPT
					9	40.59	59.02	Feb. 18	50-195	12.8	14.3	35.63	6						IYGPT
				288	22	42.15	61.16	Feb. 23	50-210	12.1	6.0	33.67	22	21	50.1	5.87	36.5	62.5	IYGPT
				388	23	41.07	61.15	Feb. 23	50-1000	10.6	4.5	33.13	4	24	48.3	9.89	25.5	59.7	IYGPT
					25	41.00	61.22	Feb. 23	50-200	10.9	6.1	33.34	17						IYGPT
					26	41.08	61.33	Feb. 23	60-200	11.6	7.0	33.78	4						IYGPT
1989	Needler	N119	Apr. 11-21	189	2-1	43.13	59.00	Apr. 12	48-199	11.0	4.8	33.13	16		67.8	12.81	46.5	96.3	IYGPT
				289	2-2	43.13	59.00	Apr. 12	48-199	11.0	4.8	33.13	33	26	43.0	10.94	23.6	60.6	IYGPT
				389	3	42.58	59.00	Apr. 13	53-202	12.0	14.6	35.62	90	59	43.0	11.65	22.5	61.9	IYGPT
				489	5	41.29	59.01	Apr. 13	402	12.0	15.5	35.82	127	60	46.1	8.85	29.0	64.7	IYGPT
				589	6-1	41.21	59.00	Apr. 14	50-192	12.0	10.6	35.84	76	52	44.8	15.14	23.4	89.7	IYGPT
				689	7	41.37	59.26	Apr. 14	56-294	11.0	14.4	35.64	82	60	55.1	14.91	25.8	89.9	IYGPT
				789	14	42.17	61.30	Apr. 17	50-203	10.0	9.3	34.22	24		80.3	7.60	64.8	98.9	IYGPT
	Needler	N122	Jun. 5-15	889	14-4	42.30	61.30	Jun. 10	46	12.5	15.5	34.32	79	60	40.6	9.37	21.6	73.0	IYGPT
		N126	Aug. 9-18	989	22	42.40	61.30	Aug. 13	47-210	8.0	21.4	32.79	147	59	44.6	3.40	37.0	52.4	IYGPT
1991	Rio Salado		Jun.	191	Set 64	43.3	64.43	Jun.29	170	9.0	11.0	-	240	58	141.4	11.6	117.5	181.4	BOT
	Rio Daruji		Jun	291	-	42.59	62.04	Jun.21	200	-	-	-	294	61	150.8	11.23	116.0	185.0	BOT
	Petrel	9108	Jul	391	6	44.24	60.58	Jul.27	114	-	-	-	63	60	156.6	10.50	138.0	191.0	Yankee

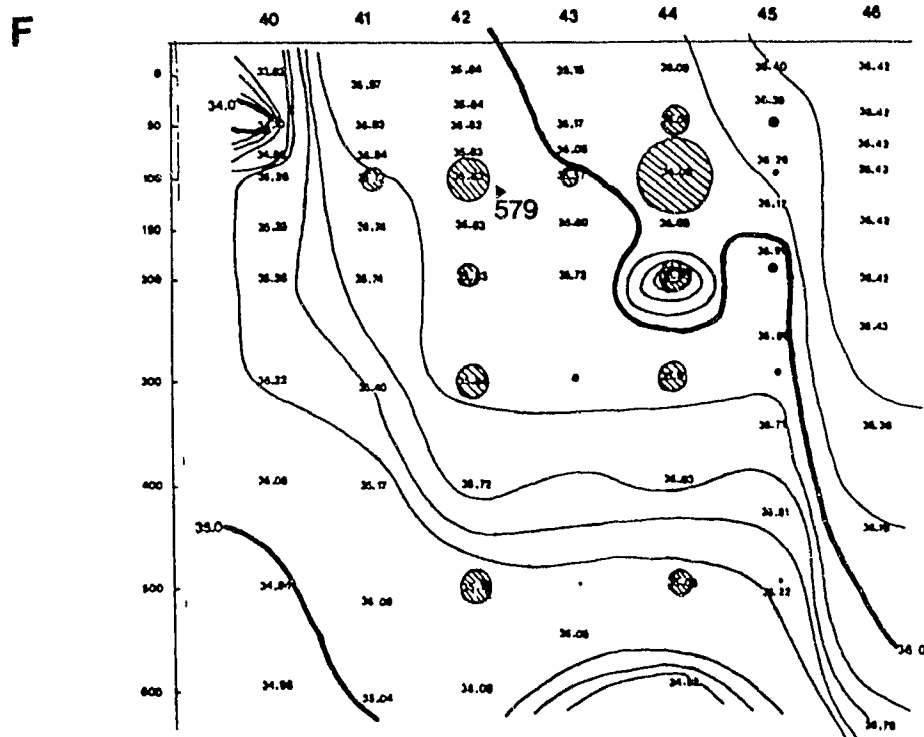
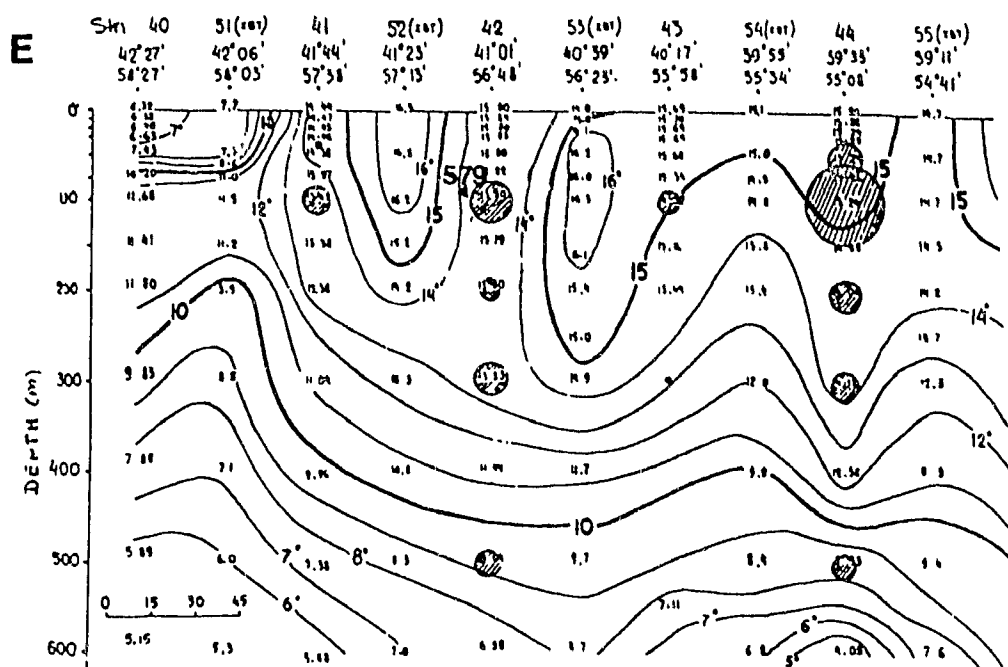
APPENDIX 2

Temperature (in °C) and salinity (in ppt.) profiles measured along the transects of the 1979 survey, reproduced from Amaratunga et al. (1980). Samples analyzed are indicated. A and B, transect 1 (March 16-18, 1979); C and D, transect 5 (March 31- April 3, 1979); E and F, transect 6 (April 4-7, 1979). Shadowed circles indicate number of squids caught in each tow.



Transect 1 (March 16-18, 1979)





Transect 6 (April 4-7, 1979)

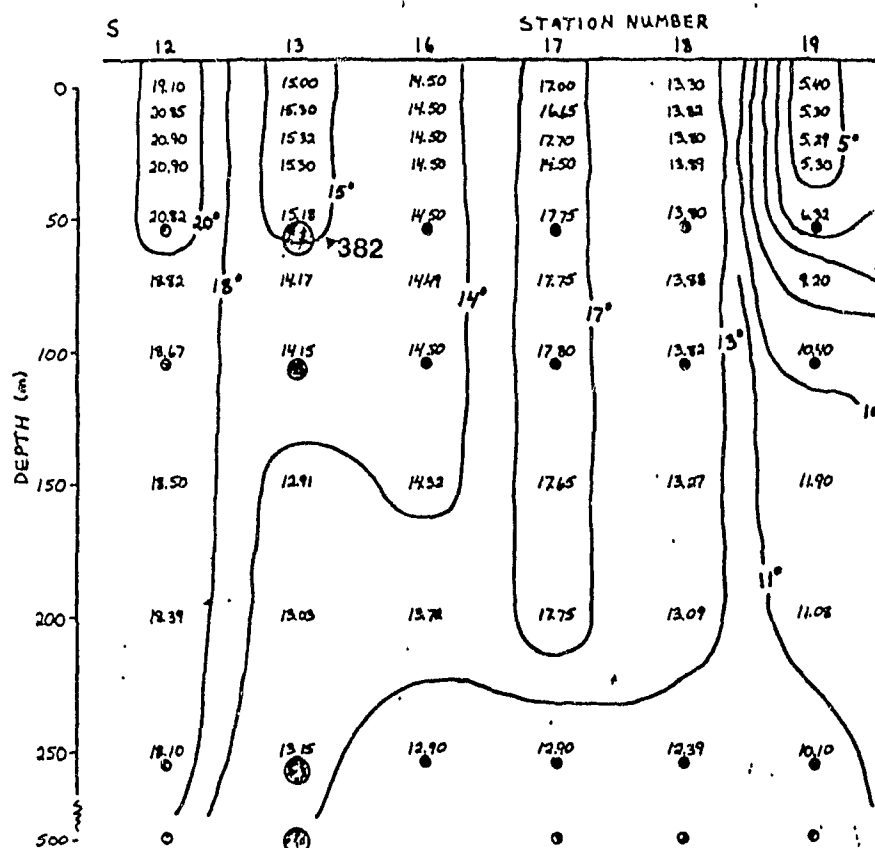
APPENDIX 3

Temperature (in °C) and salinity (in ppt.) profiles measured along the transects of the 1981 survey (Feb. 21- Mar. 06), reproduced from Dawe and Beck (1985). Samples analyzed are indicated. A, transect A; B, transect B. The number of squids caught in each tow are indicated.

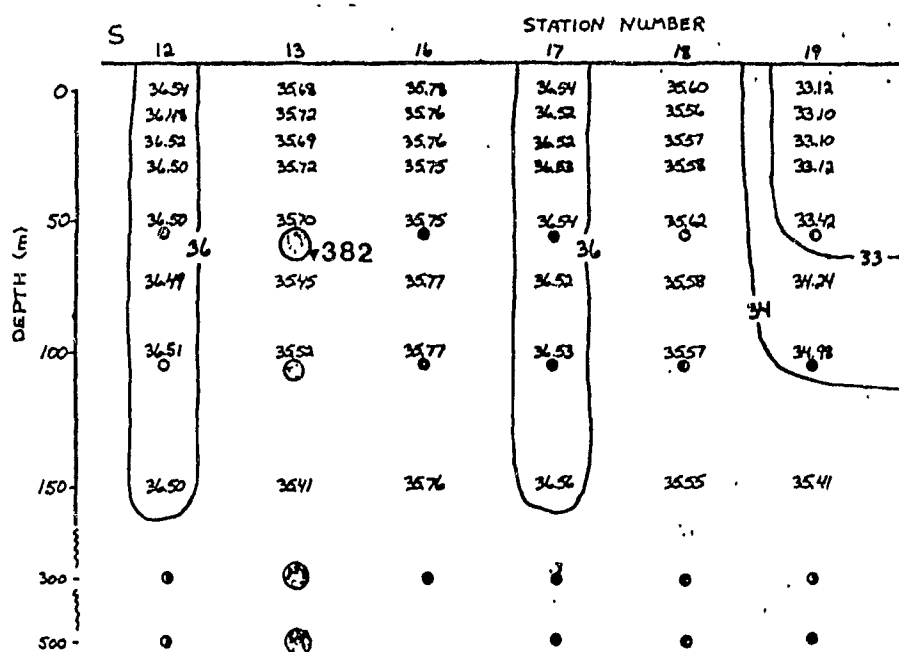
APPENDIX 4

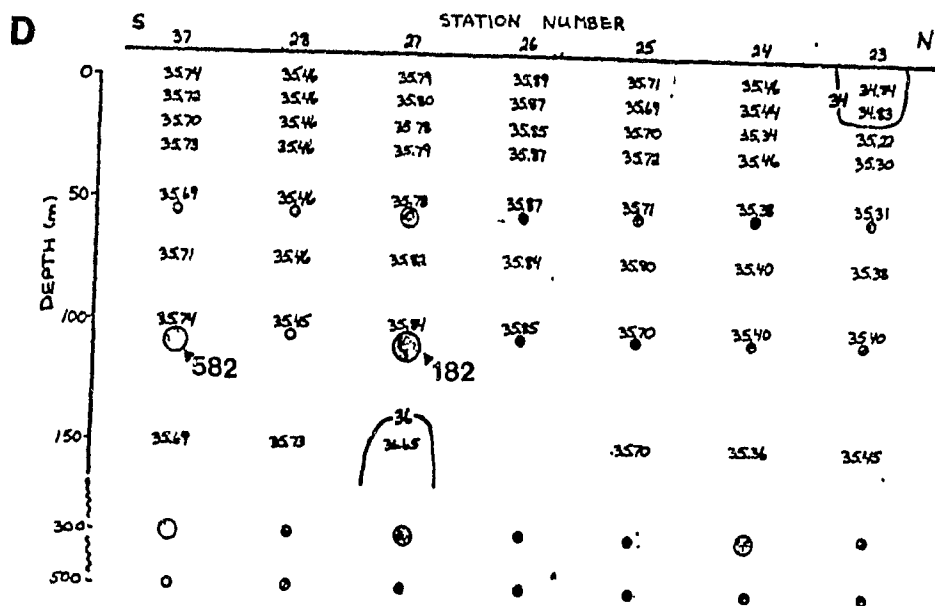
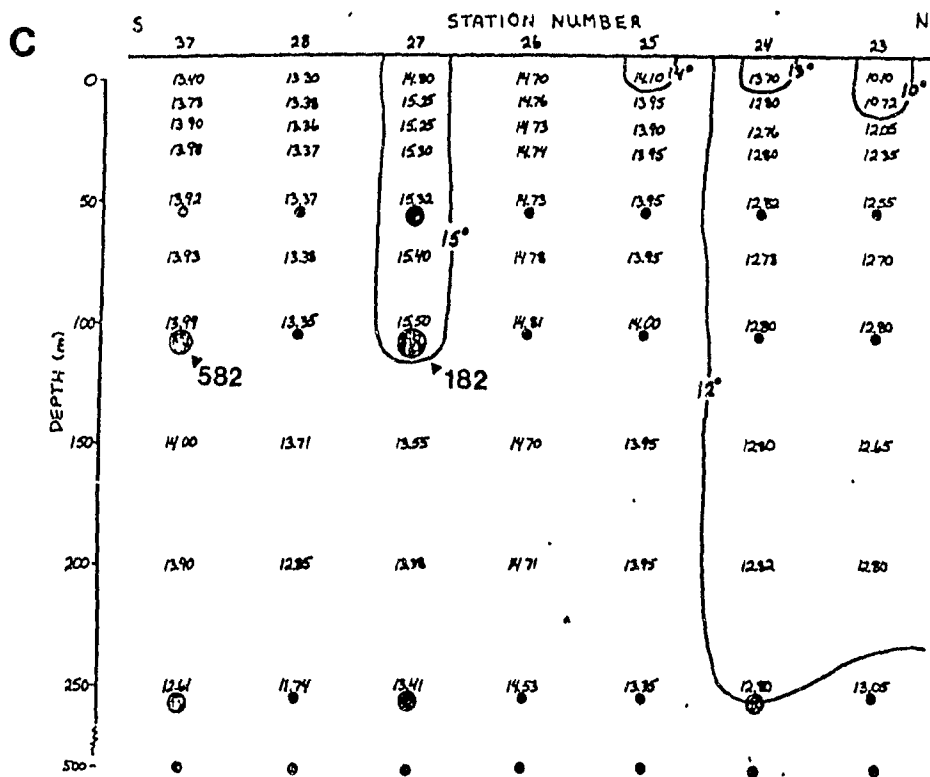
Temperature (in °C) and salinity (in ppt.) profiles measured along the transects of the 1982 survey (Feb. 2-25), reproduced from Amaratunga and Budden (1982). Samples analyzed are indicated. A and B, transect 2; C and D, transect 3; E and F, transect 4. Shadowed circles indicate number of squids caught in each tow.

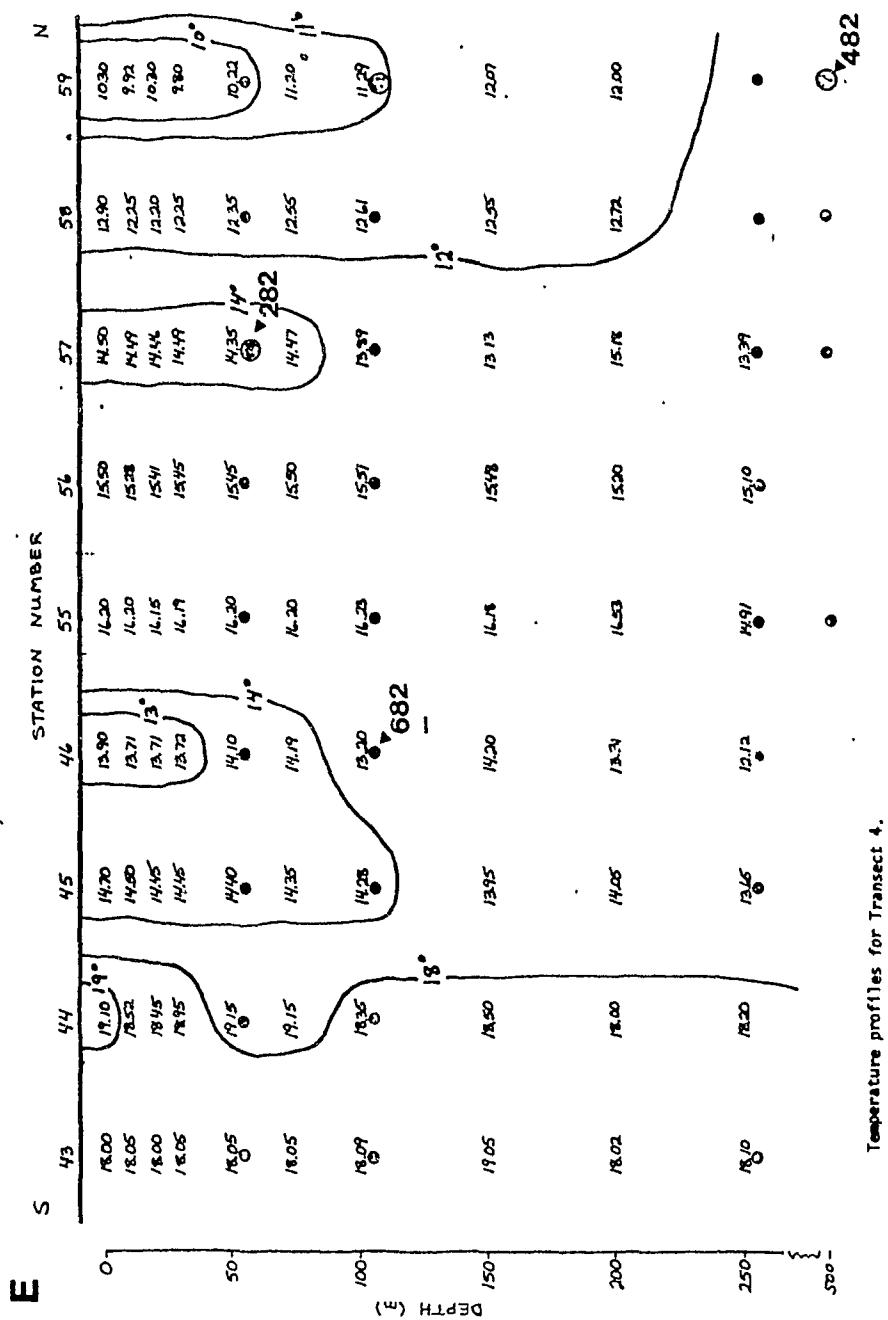
A

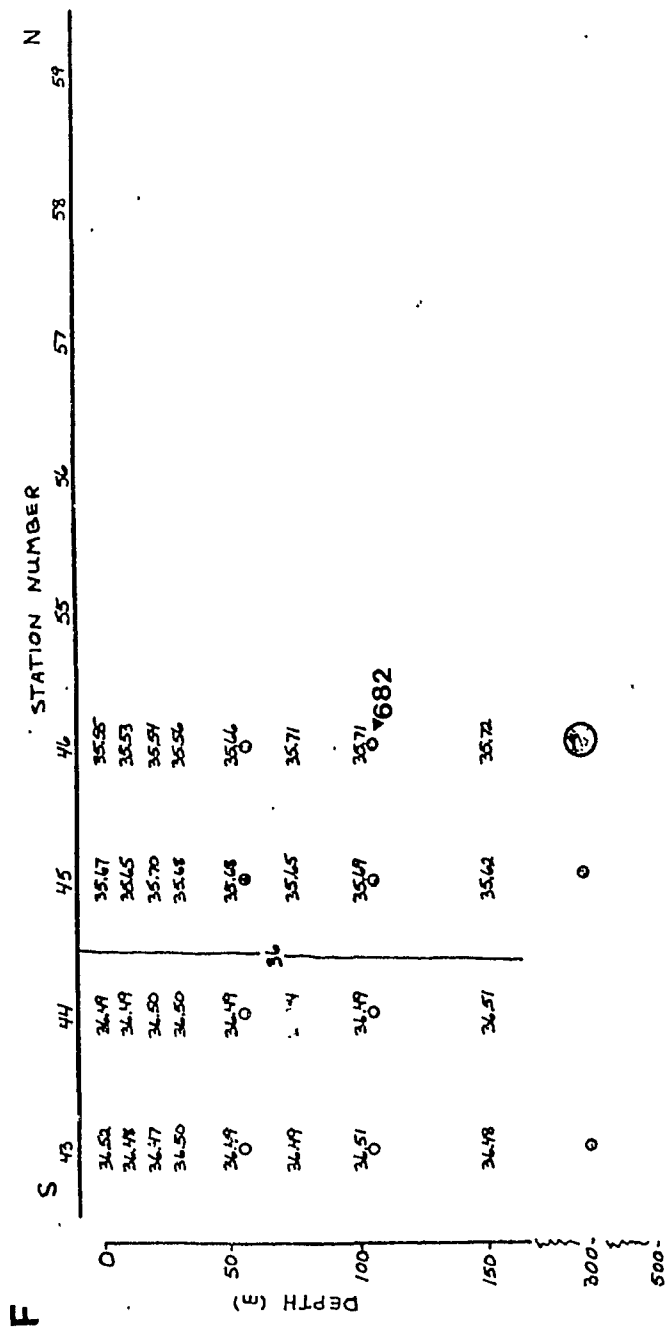


B





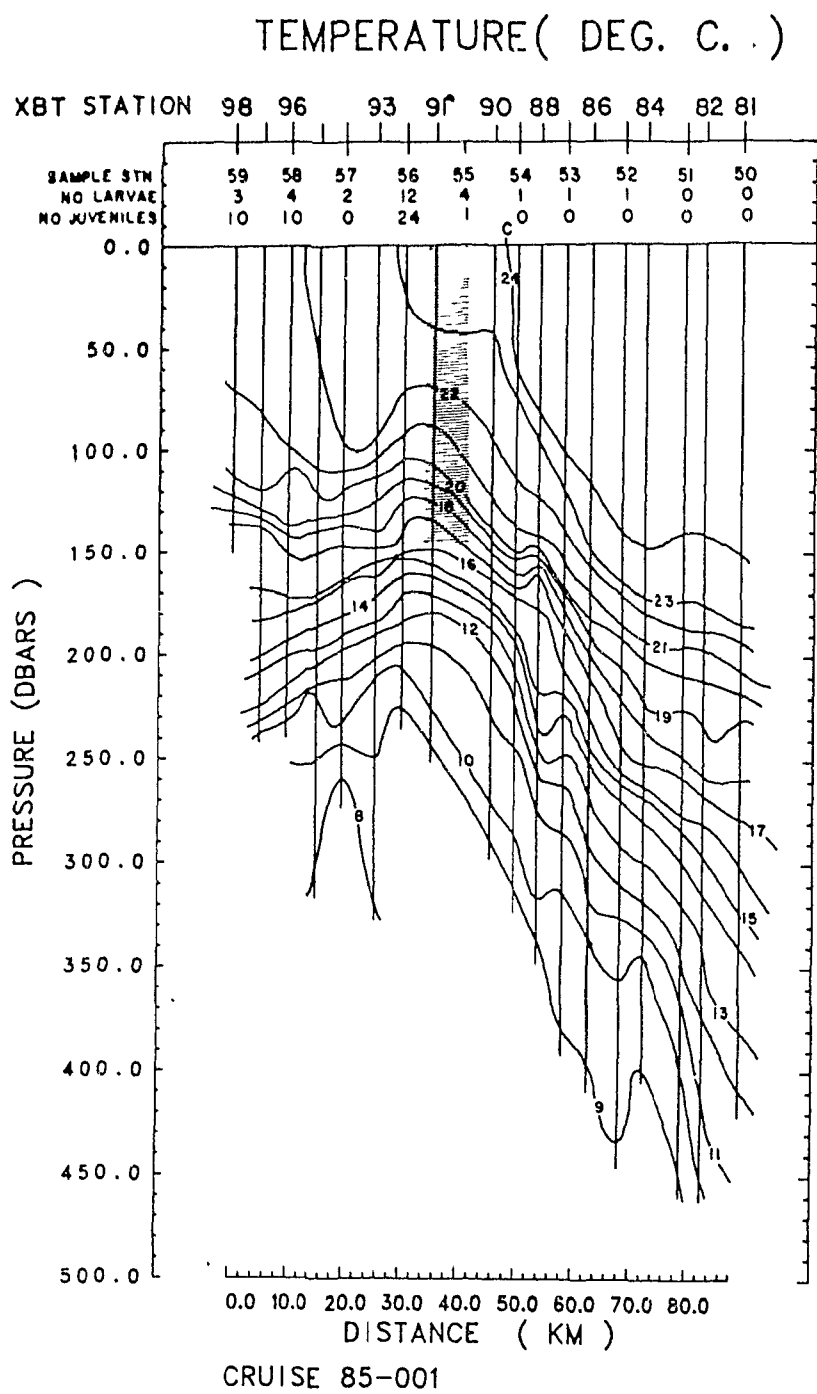




APPENDIX 5

Temperature (in °C) profiles measured along the transects of the 1985 survey (Jan. 7-22), reproduced from Trites and Rowell (1985). Samples analyzed are indicated. A, transect III (13-14 Jan.); B, transect V (20-21 Jan.). Shadowed areas indicate the depth range sampled.

A

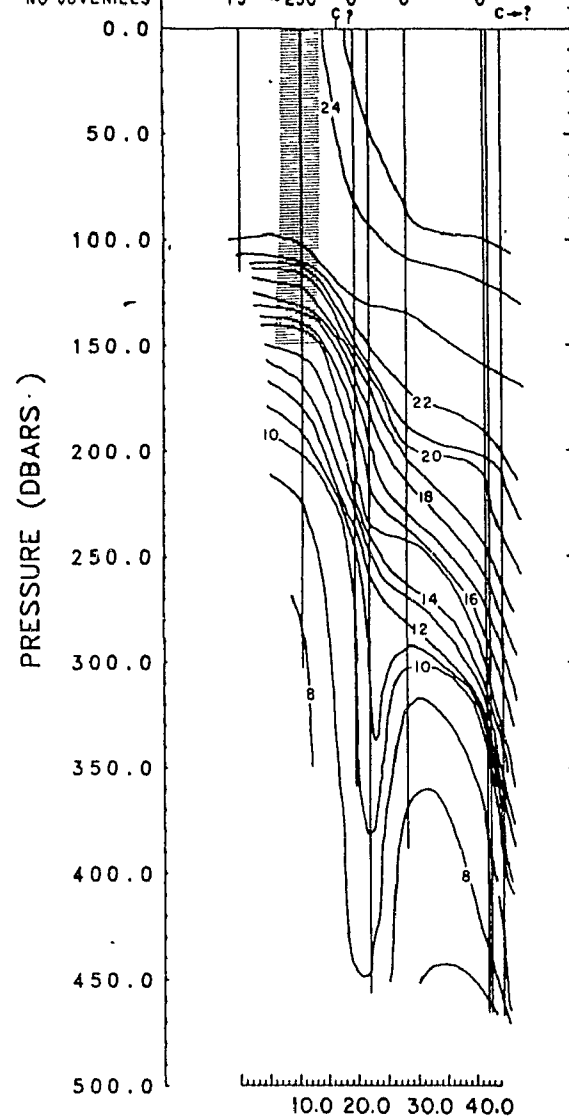


B

TEMPERATURE (DEG. C.)

XBT STATION 163 162 161 159 156

SAMPLE STN	99	98	97	96	9594
NO LARVAE	3	6	4	4	0
NO JUVENILES	15	~250	0	0	0

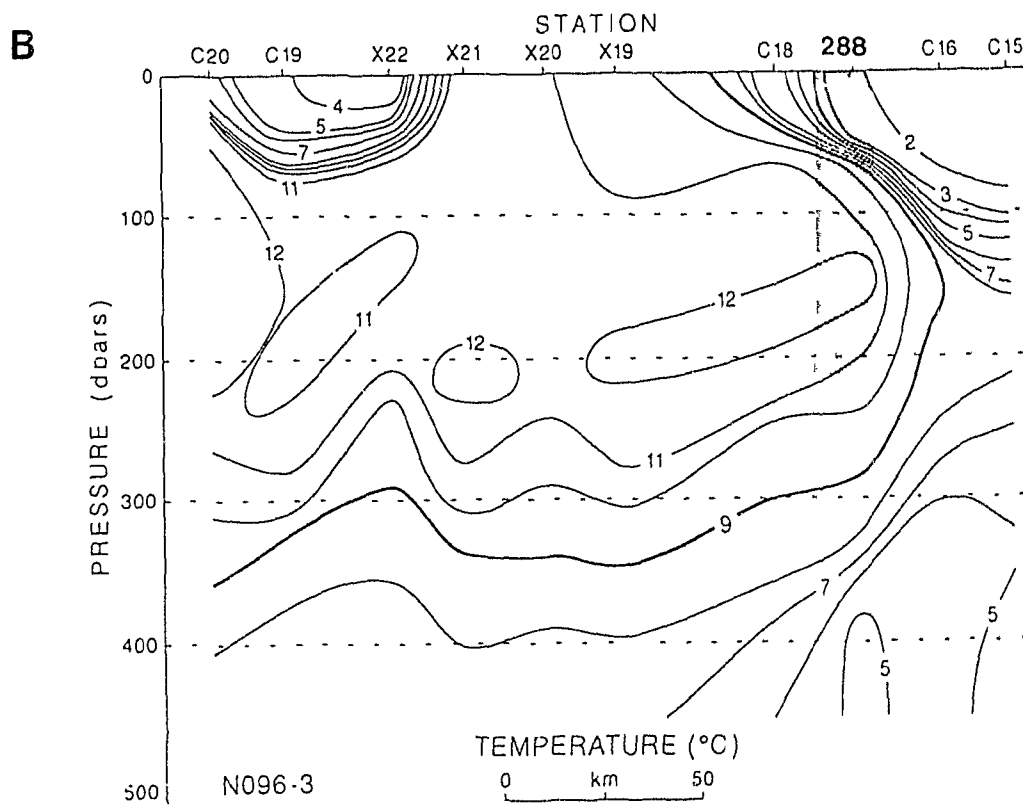
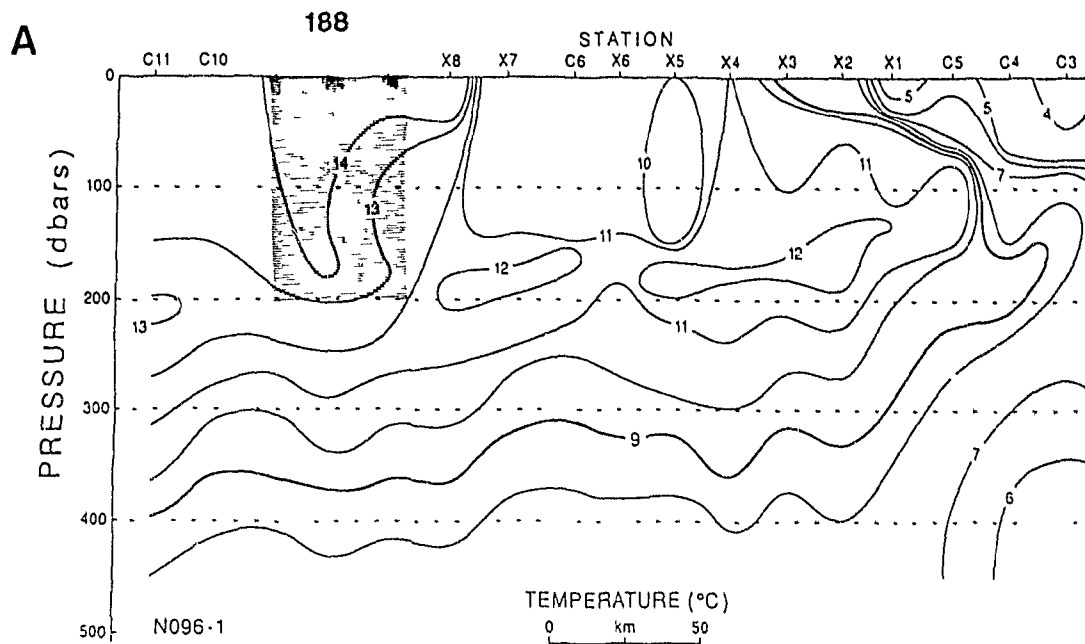


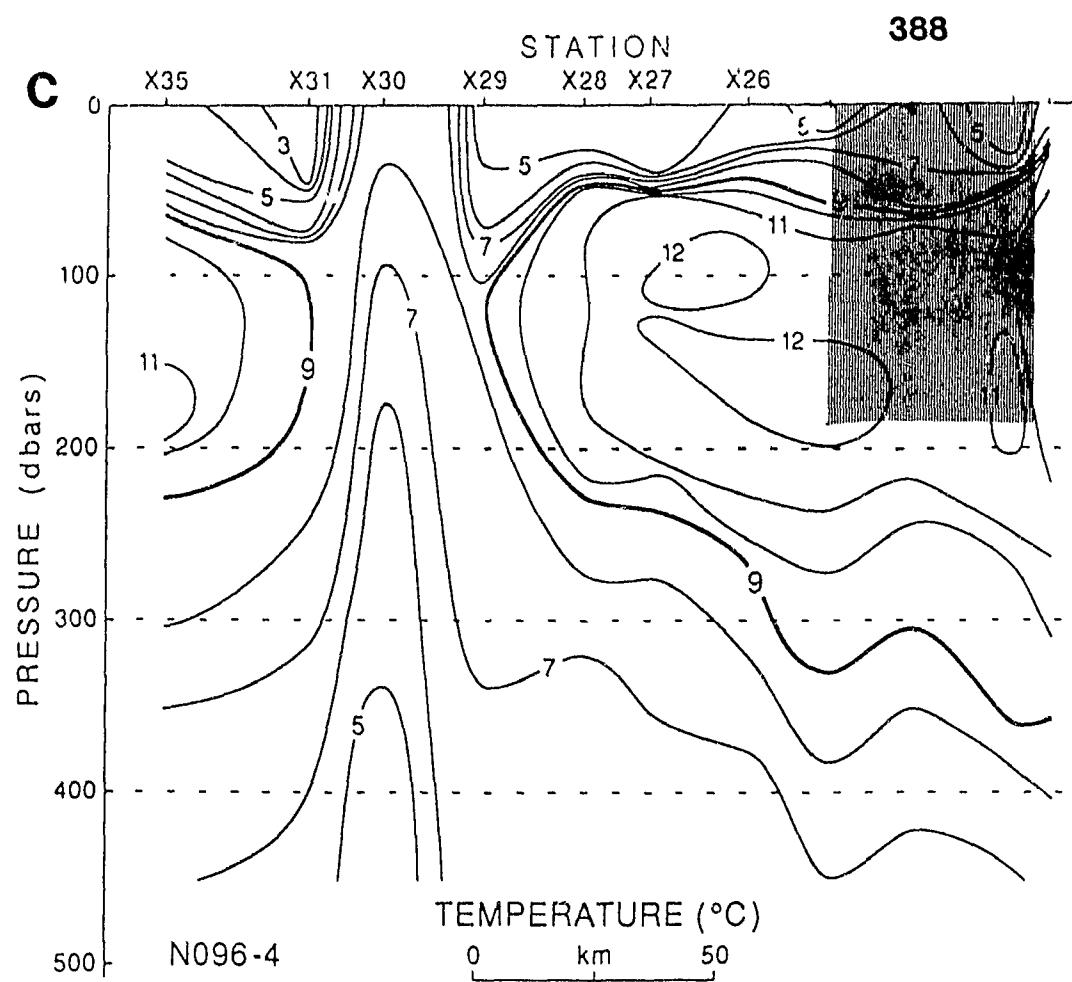
DISTANCE (KM)

CRUISE 85-001

APPENDIX 6

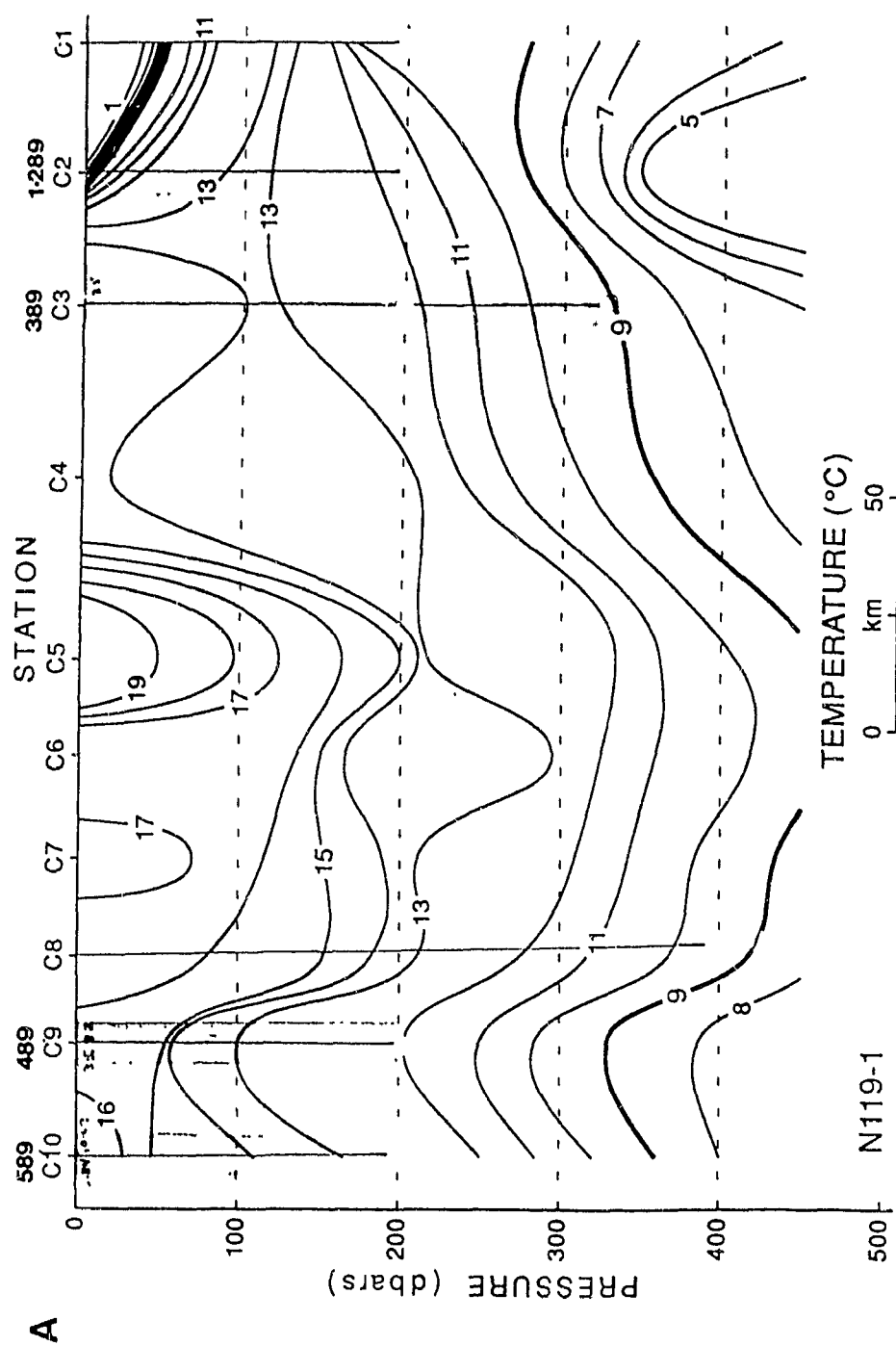
Temperature (in °C) profiles measured along the transects of the 1988 survey (Feb. 15-26). Samples analyzed are indicated. A, transect 1; B, transect 3; C, transect 5. Shadowed areas indicate the depth range sampled.

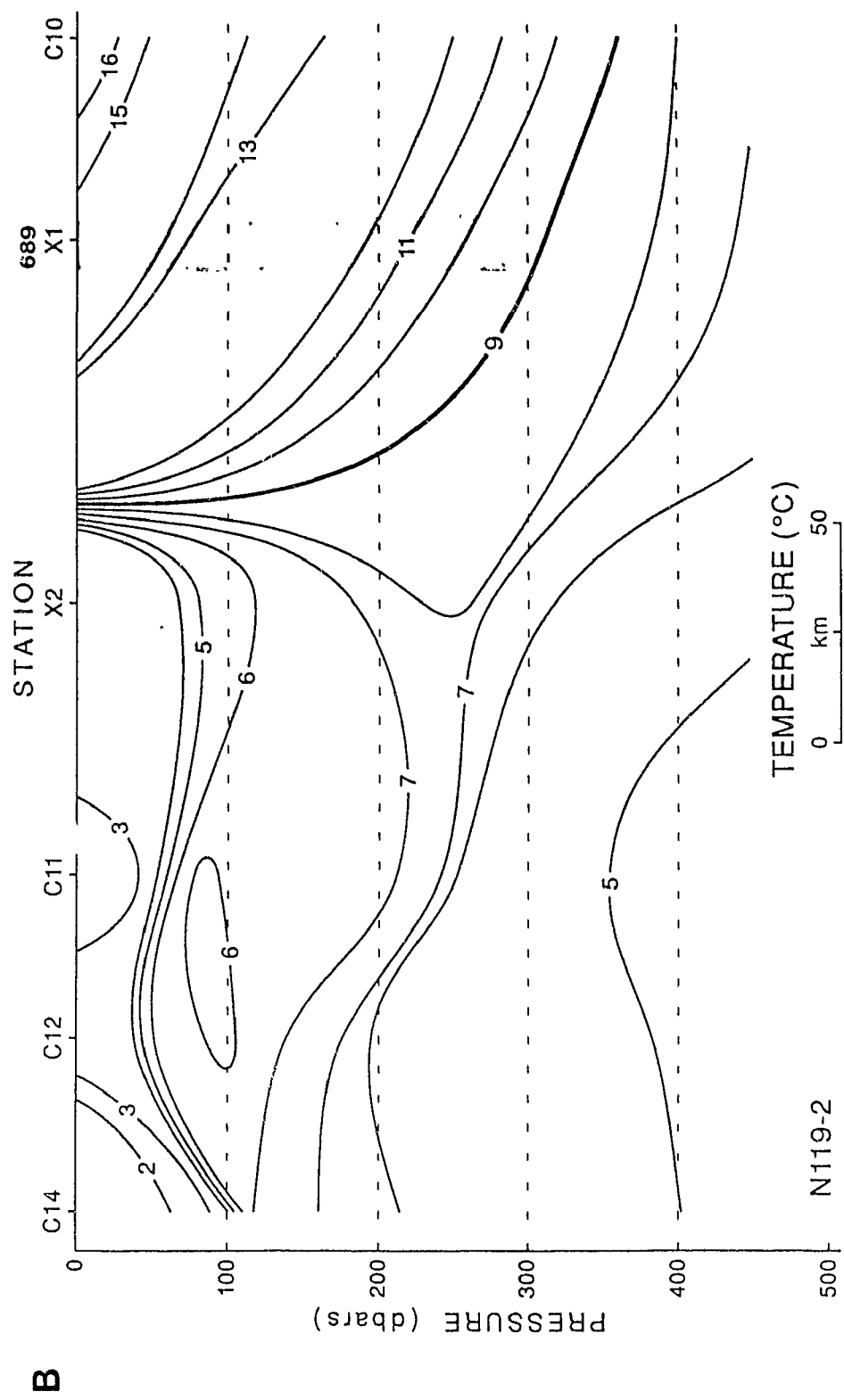


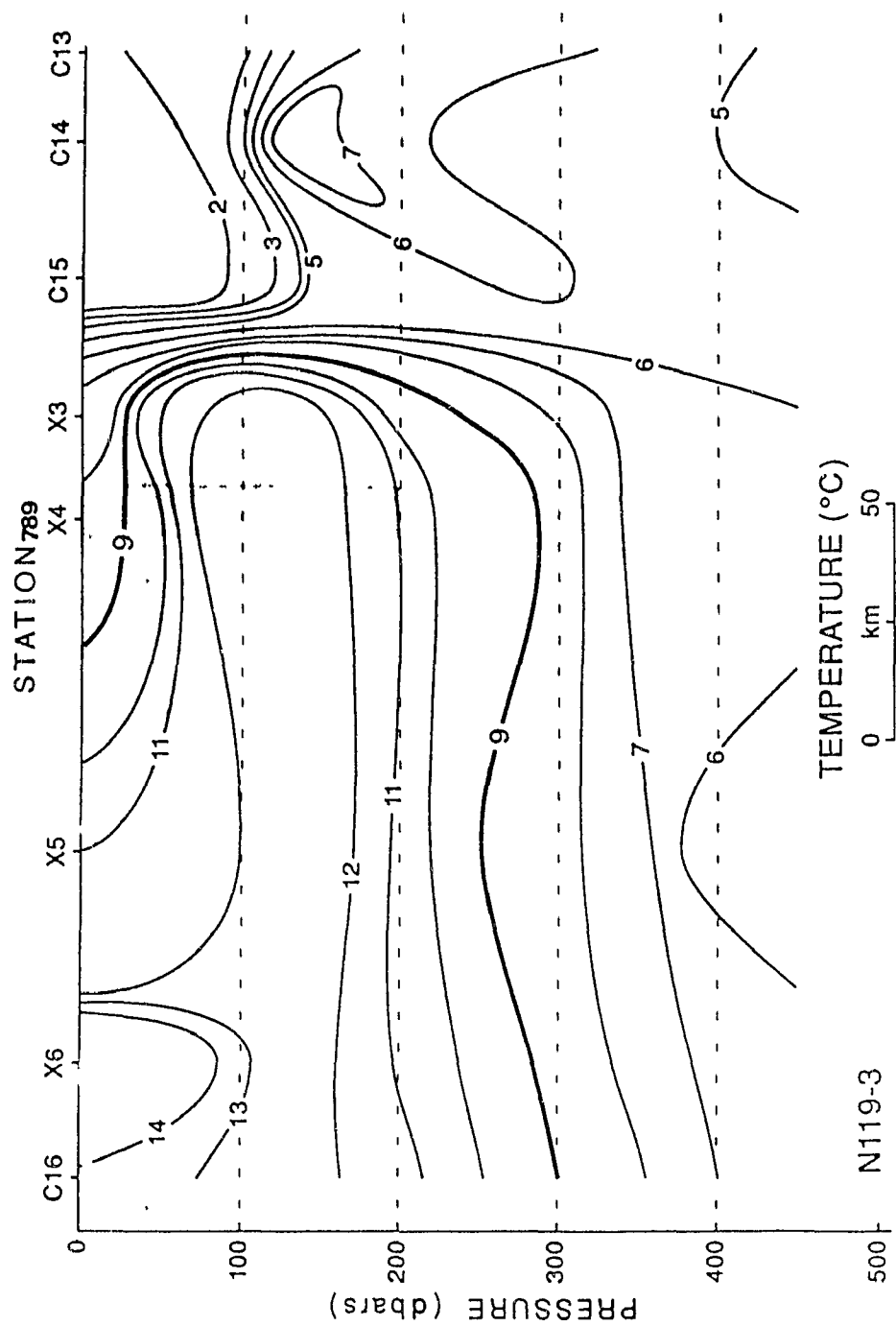


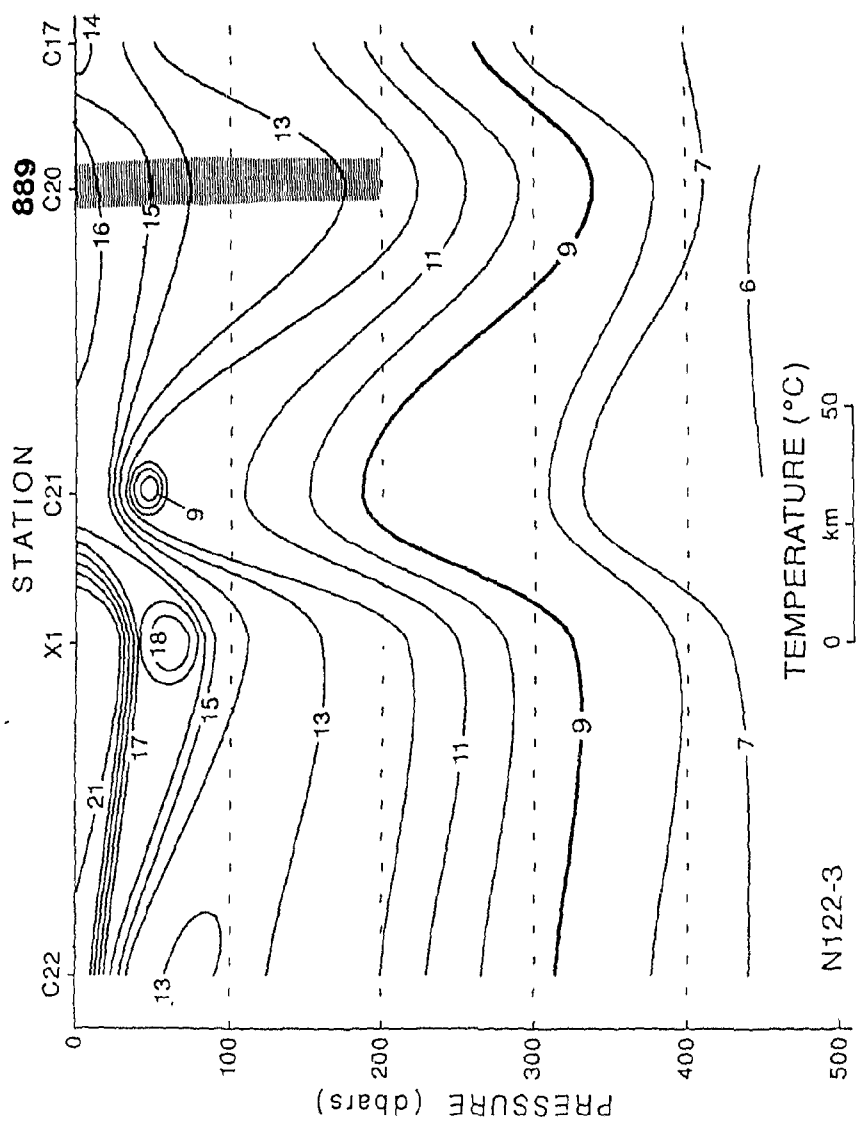
APPENDIX 7

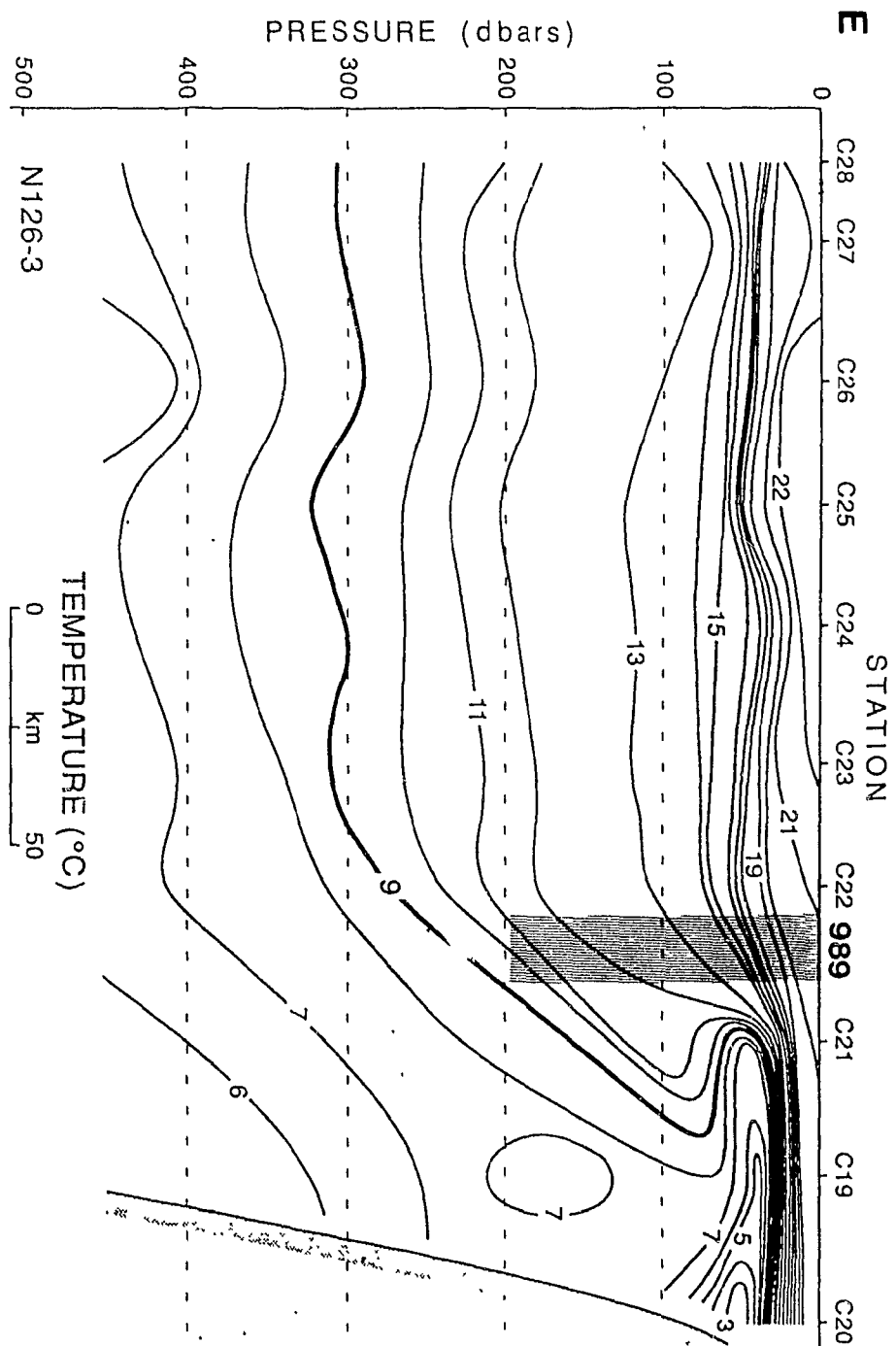
Temperature (in °C) profiles measured along the transects of the 1989 surveys (N119 - Apr. 11-21; N122 - Jun. 5-15; N126 - Aug. 9-19). Samples analyzed are indicated. A, transect 1 (N119); B, transect 2 (N119); C, transect 3 (N119); D, transect 3 (N122); E, transect 3 (N126). Shadowed areas indicate the depth range sampled.











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