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DISTRIBUTION OF LARVAL AND JUVENILE *ILLEX* (MOLLUSCA : CEPHALOPODA) IN THE BLAKE PLATEAU REGION (NORTHWEST ATLANTIC)

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CEPHALOPODA
SQUID
ILLEX
LARVAL
JUVENILE
DISTRIBUTION
OCEANOGRAPHY

ABSTRACT. — Knowledge of the distribution of larval and juvenile short-finned squid *Illex illecebrosus* has increased rapidly since 1979 when the first large catches of these early life stages were taken along the northern edge of the Gulf Stream and in the adjacent Slope Waters between approximately 66° and 44°W. The role of the Gulf Stream system in the entrainment, transport, and dispersion of larval and juvenile *Illex* is discussed and recent evidence is presented for the existence of a major spawning area shoreward of the Gulf Stream Frontal Zone over the Blake Plateau. Larval and juvenile sizes and distribution patterns are analyzed in relation to macro- and meso-scale oceanographic features of the Gulf Stream Frontal Zone. Information is provided on meso-scale distributional differences between larvae and juveniles of *Illex* and also between various types of Rhynchoteuthion larvae.

CEPHALOPODA
ENCORNET
ILLEX
LARVE
JUVÉNILE
DISTRIBUTION
OCÉANOGRAPHIE

RÉSUMÉ. — Les connaissances sur la répartition de l'Encornet rouge, *Illex illecebrosus* aux stades larvaire et juvénile ont augmenté rapidement depuis 1979, c'est-à-dire depuis les premières récoltes importantes à des stades de vie précoces. Les prises ont eu lieu le long de la bordure nord du Gulf Stream et dans les eaux adjacentes du talus continental, entre 66° et 44 °W approximativement. Le rôle du Gulf Stream dans l'entraînement, le transport et la dispersion des Encornets larvaires et juvéniles est montré et des données récentes indiquant l'existence d'une zone de ponte importante du côté continental de la Zone frontale du Gulf Stream, sur le plateau de Blake, sont présentées. Les caractéristiques relatives à la taille et à la répartition des Encornets larvaires et juvéniles en fonction des caractéristiques océanographiques à grande et à moyenne échelle de la Zone frontale du Gulf Stream sont analysées. Enfin des informations indiquant des différences de répartition larvaire et juvénile entre les Encornets du genre *Illex* et d'autres larves de type Rhynchoteuthion sont présentées.

INTRODUCTION

The short-finned squid *Illex illecebrosus* is highly important to the fisheries of the northwest Atlantic both as a harvestable resource and as a major predator and prey species. Because of its relatively short life-cycle, estimated at 1-1.5 years (Squires, 1967), conventional methods of biomass projection have been impossible, as has the application of conventional fisheries management practise. Recognition of the need to develop a biological basis for management of the resource has led, since 1979, to major research efforts being directed at determining the essentially unknown early life history and distribution of the species. Prior to this, knowledge of the biology and distribution of *I. Illecebrosus* was largely restricted to the adult stage, from May through December, during the residency period on the shelf (Verrill, 1882; Mercer, 1969a, 1969b, 1973; Squires, 1967; Lange, 1980).

O'Dor (1983) has summarized the general biology and ecology of *I. illecebrosus,* while Rowell *et al.* (1984) and Trites and Rowell (1985) have reviewed the historical development of knowledge on the early life stages as well as recent research directed at determining the influence of oceanographic processes on their distribution. The discovery, during the winter of 1979 (Amaratunga *et al.,* 1980; Fedulov and Froerman, 1980), of large concentrations of small juveniles (approximately 15-80 mm Dorsal Mantle Length), as well as some larvae, between the Gulf Stream and the edge of the Scotian Shelf provided the first strong evidence in support of the suggestion of Roper & Lu (1979) that the Gulf Stream might play a role in the life-cycle of *I. illecebrosus.* Surveys in subsequent years provided additional distributional information and indicated that spawing probably occured upstream in the area south of, or immediately to the north of Cape Hatteras. Trites (1983) developed a larval dispersion model that would predict an idealized distribution of larval and early juvenile stages over a 1-2 month period after spawning. The model assumed bottom spawning, but appears equally valid for the pelagic spawning that we now consider more likely. Under this model, egg masses, larvae, and possibly juveniles are entrained by the Gulf Stream and transported at variable speed northeastward to areas seaward of the Continental Shelf along the northeastern U.S.A., the Scotian Shelf, and Grand Banks. During the course of this transport, the juveniles either passively, along with Warm Core Eddy formation, or actively leave the High Velocity Core of the Gulf Stream as it progresses northeastward and subsequently actively migrate shoreward to the Continental Shelf. Beginning in January 1983 a series of cruises was begun to examine the advection scenario as a mechanism for the transport of larvae and juveniles from assumed spawning areas over the Blake Plateau to the offshore area south of the Scotian Shelf and Grand Banks.

This paper provides a synoptic description of the distribution of Rhynchoteuthion type C' larvae and juveniles (Roper and Lu, 1979), believed to be *Illex illecebrosus,* in relation to the Gulf Stream and adjacent Slope Waters. Data are presented suggesting close proximity of a major spawning area to the region of Cape Canaveral, Florida. Information is also provided on the distribution of Rhynchoteuthion larval types A' and B' (Roper and Lu, 1979), believed to be *Ommastrephes bartrami,* and *Ornithoteuthis antillarum* and/or *Ommastrephes pteropus* respectively.

MATERIALS AND METHODS

Since March 1979 there has, in most years, been extensive sampling of the Gulf Stream and Slope Waters off the Scotian Shelf and Grand Banks between roughly 66° an 44 °W longitude.

There has been much less extensive sampling specifically directed at larval and juvenile *Illex* west of 66 °W. Dawe and Beck (1985) reviewed the distribution of larval *Illex* catches, including those from this more westerly area, for the period up to 1982, while Hatanaka *et al.* (1982) presented distributional information for both larvae and juveniles as far west as 74 °W. This paper draws on all of the available sources, including Amaratunga *et al.* (1980); Amaratunga & Budden (1982); Dawe *et al.* (1982); Fedulov *et al.* (1984). Data are also extracted from Rowell *et al.* (1984); and Trites and Rowell (1985) which include surveys by : the Alfred Needler, 28 January — 2 March 1983; the CSS Hudson, 11-15 December, 1984; and the Alfred Needler, 7-22 January 1985, and subsequently referred to in this paper respectively as Needler 83, Hudson 84 and Needler 85.

OCEANOGRAPHIC FEATURES AND DISTRIBUTIONAL PATTERNS OF EARLY LIFE STAGES

General Oceanographic Features

A dominant oceanographic feature in the North Atlantic is the Gulf Stream System, an intense western ocean boundary current present from the Straits of Florida to an area southeast of the Grand Banks (Fig. 1). Off the east coast of Florida the shoreward edge of the Gulf Stream (Slope/Gulf Stream Front), on average, can be delineated ap-

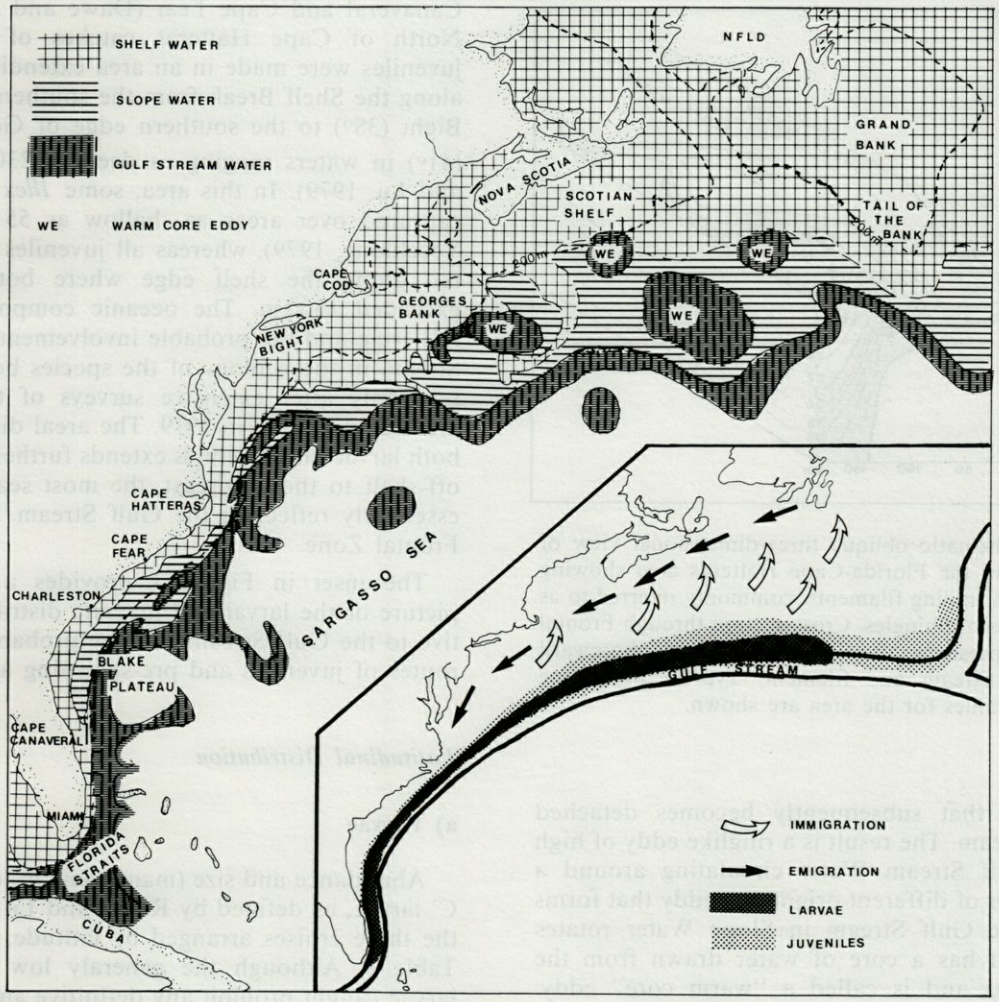


Fig. 1. — Map showing the Gulf Stream system off eastern North America, and major surface water-mass features for 4-5 January, 1985, (Extracted from United States National Weather Service NOAA/NESS satellite-derived oceanographic analysis maps). A schematic illustration of the suggested general life-cycle of *Illex illecebrosus* in relation to the Gulf Stream is shown in the inset.

proximately by the 200 m isobath. Further north, off South Carolina, the Stream tends to move further offshore, returning to about the 200 m isobath a short distance south of Cape Hatteras. Northeast of Cape Hatteras the Stream moves off the continental slope. The position of the Stream fluctuates.

Analysis of sea surface temperature maps, reveals that the standard deviation in the position of the Slope/Gulf Stream Front increases from a minimum of about 5 km off the east coast of Florida to a maximum of about 35 km off Cape Fear and then decreases to about 10 km off Cape Hatteras (Bane and Brooks, 1979). Downstream from Cape Hatteras, the amplitude of the meanders again increases rapidly, with the position of the northern edge of the Stream south of Nova Scotia varying by as much as 400 km.

In the Straits of Florida-Cape Hatteras area, the shoreward boundary of the Stream displays, in addition to meanders, a folded-wave pattern of Frontal Eddies (Fig. 2). Frontal Eddies of this type appear as tongue-like extrusions (filaments) of Gulf Stream Water, oriented upstream, nearly parallel to the Stream (and bathymetry). These Frontal Eddies tend to develop near the shoreward crest of a meander and usualy grow rapidly, developing a narrow, very elongated filament or "shingle" appearance (Lee *et al.*, 1981; Legeckis, 1979; Bane *et al.*, 1981). Frontal Eddies are short-lived phenomena, forming in only a few days and possibly dissipating on a comparable time scale. Satellite sea surface thermal imagery suggests that the total cycle takes place in 1 to 3 weeks, with wavelengths ranging from 90 to 260 km, and moving at speeds from 20 to 60 km/d in the general direction of the Gulf Stream (Legeckis, 1979).

Downstream from Cape Hatteras, the large meanders which develop in the Stream may form a

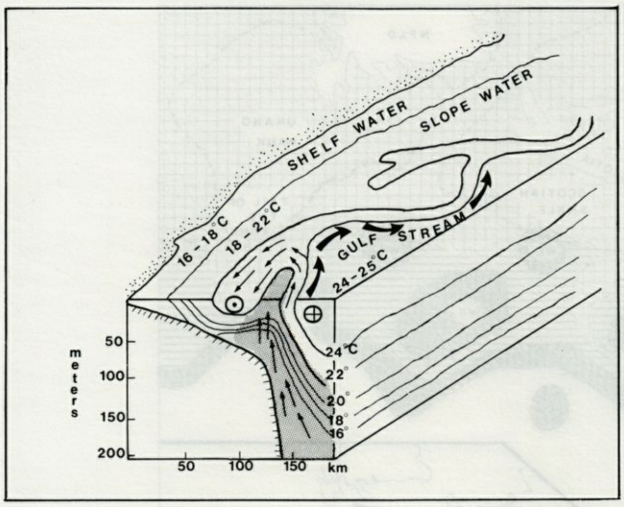


Fig. 2. — Schematic oblique three-dimensional view of Gulf Stream in the Florida-Cape Hatteras area showing meanders with trailing filaments, commonly referred to as Frontal Eddies or Shingles. Cross-section through Frontal Eddy shows presence of cold dome between shoreward edge of the Stream and filament. Typical wintertime temperature values for the area are shown.

major loop that subsequently becomes detached from the stream. The result is a ringlike eddy of high velocity Gulf Stream Water circulating around a core of water of different origin. An eddy that forms north of the Gulf Stream in Slope Water rotates clockwise; it has a core of water drawn from the Sargasso Sea and is called a "warm core" eddy. Warm Core Eddies, have a life-span that may vary from a few weeks to a year or more, and range in diameter from about 100 km up to 300 km.

The possible importance, as a transport-dispersion mechanism, of both the Gulf Stream, from Cape Hatteras northeastward, and the associated Warm Core Eddies have been examined by Trites (1983) in determining the distribution of larval/juvenile *Illex*. This paper will focus primarily on the distribution of early life stages of *Illex* in the area extending from Cape Hatteras southwestward to the Straits of Florida where the Gulf Stream and associated frontal eddies may play a key role.

General Distributional Patterns

General distributional knowledge of the early life stages of *Illex illecebrosus* has increased dramatically in recent years. The distributional information available prior to 1979 was all from areas either on the Continental Shelf or immediately along the Shelf Break suggesting an essentially neritic life-cycle. South of Cape Hatteras catches of larvae and juveniles were limited to an area along the 200 m isobath over the Blake Plateau between roughly Cape Canaveral and Cape Fear (Dawe and Beck, 1985). North of Cape Hatteras catches of larvae and juveniles were made in an area extending generally along the Shelf Break from the southern New York Bight (38°) to the southern edge of Georges Bank (41°) in waters ranging as deep as 2300 m (Roper and Lu, 1979). In this area, some *Illex* larvae were captured over areas as shallow as 55 m (see also Vecchione, 1979), whereas all juveniles were captured along the shelf edge where bottom depths exceeded 1500 m. The oceanic component of the life-cycle and the probable involvement of the Gulf Stream in the ecology of the species became apparent only after extensive surveys of the off-shelf areas commenced in 1979. The areal distribution of both larvae and juveniles extends further and further off-shelf to the northeast, the most seaward extent essentially reflecting the Gulf Stream/Slope Water Frontal Zone.

The inset in Figure 1 provides a generalized picture of the larval and juvenile distributions relative to the Gulf Stream and the probable migration routes of juveniles and pre-spawning adults.

Latitudinal Distribution

a) Larvae

Abundance and size (mantle length) data for type C' larvae, as defined by Roper and Lu (1979), from the three cruises arranged by latitude, are given in Table I. Although the generaly low numbers of larvae caught prohibit any definitive analysis, qualitatively, larvae are generally less abundant or are absent in the more northeasterly stations (Cape Hatteras area), as compared to the central area (off Charleston) with maximum catches taken in the Cape Canaveral area in the Needler 85 survey (Transect IV). Catch rates (Table IIA) are also low in the northeast and high along Transect IV. There is no clear geographical variation in size distribution. For the Hudson 84 and Needler 85 data there is some evidence of an increase in the median larval mantle lenght (ML) as well as an increase in minimum mantle lengths from southwest to northeast. In the more limited Needler 83 data there is a weak suggestion of the reverse during Leg I of the cruise, whereas Leg II data show smaller larvae to the south of those stations occupied in Leg I. These smaller lavae might represent a second brood. Sufficient numbers of larvae for lenght frequency histograms were taken only in Transects III, IV, and V on the Needler 85 survey and at a 22-h drogue-drift station located near Transect IV (Fig. 3). The most symmetrical distribution, with smallest size range, is found at and near Transect IV, with a strong mode at 1.8-1.9 mm ML. At Transects III and V the distribution is much flatter and has a wider range of sizes.

Table I. — Number and size (mantle length in mm) of Rhynchoteuthion type C' larvae in relation to latitude in February, 1983; December, 1984; and January, 1985.

	Needler (Feb. 83)				Hudson (Dec. 84)				Needler (Jan. 85)			
Latitude	Station No.	No. of Larvae	Mantle Range (mm)	Median Length (mm)	Station No.	No. of Larvae	Mantle Range (mm)	Median Length (mm)	Transect No.	No. of Larvae	Mantle Range (mm)	Median Length (mm)
Northeast												
36°00'N									I	2	3.2-6.4	4.8
35°00'					23	4	2.3-3.1	2.7				
34°41'					21	1	4.2	4.2				
34°30'									II	3	1.1-6.3	4.6
34°23'					20	1	2.4	2.4				
33°58'	44	1	2.5	2.5								
33°53'					18	1	1.8	1.8				
33°42'	53	2	3.5-4.8	4.1								
33°37'					16	1	2.2	2.2				
33°30'					15	2	2.0-2.7	2.4				
33°22'	65	3	3.5-3.9	3.7								
33°19'	66	1	3.5	3.5								
33°12'					13	1	1.8	1.8				
33°03'	69	1	3.0	3.0								
32°46'	82	1	3.0	3.0								
32°42'	83	2	3.0-4.9	3.9								
32°30'									III	39	0.8-6.0	1.8
32°17'	95	2	3.5-3.9	3.7								
32°12'					7	6	1.8-2.6	2.0				
32°11'	92	1	4.0	4.0								
32°11'					5	3	1.0- 2.0	1.8				
32°10'					6	3	1.0->1.7	1.6				
32°08'	88	1	3.3	3.3								
32°06'	106	1	>3.5	>3.5								
32°01'	107	3	2.8-6.4	3.2								
32°00'					4	7	2.2-3.8	2.6				
31°57'	108	3	3.0-5.4	5.0								
31°51'					3	23	1.6-4.2	2.2				
31°40'					2	2	>0.8-2.2	1.5				
31°23'	122	1	4.8	4.8								
31°13'	51*	1	1.0	1.0								
30°53'	131	1	>4.0	>4.0								
30°50'	129	1	>4.0	>4.0								
29°49'	8*	1	3.0	3.0								
28°50'	27*	2	1.0-2.0	1.5								
28°43'	33*	1	2.0	2.0								
28°30'									IV	123	1.0-3.4	2.0
25°25'									V	40	0.8-5.6	1.8
Southwest												

*Needler (Feb. 83 - LEG II)

b) Juveniles

The Needler 83 survey shows juvenile abundance to be highly variable latitudinally with no clear pattern, whereas the Needler 85 data reveal much higher numbers (and catch rates) in the southern three transects, being highest at Transect III (Tables IIA and III). We note that, if the high catch at station 45 of Transect III is deleted, catch rate increases progressively from Transects I through V. Interestingly, although the percentage of stations with catch shows little variation throughout the entire area, there appears to be a general progression as one proceeds southwestward. Although neither the 1983 nor the 1985 surveys provide any clear indication of a latitudinal progression in size of juveniles, the 1983 data do suggest the possiblity of increasing size towards the southwest when the median values for those stations having larger catches (⩾ 15) are examined. In terms of length frequency patterns, the most peaked distribution occurred at Transect IV (Fig. 3).

Distribution Normal to the Gulf Stream Axis

The Needler 83 survey was designed to make many transverse sections approximately normal to the axis of the Gulf Stream (Fig. 4 A). The 15 °C isotherm, which is usually nested within a closely spaced set of isotherms at 200 m (Worthington, 1954; Webster, 1961; Fuglister, 1963) is frequently taken to indicate the geographic position of the High Velocity Core of the Gulf Stream. Stations where a catch of larvae and/or juveniles were made on Leg I of the Needler 83 survey (Fig. 4 C) were always located shoreward of the High Velocity Core of the

Table II. — Percentage of tows which collected *Illex*, catch rate, and ratio of larvae to juveniles from Needler 1985 survey; A) by complete transects; B) by segment of transect shoreward of the High Velocity Current (HVC), and; C) by segment of transects in the HVC.

A

Transect	Percentage of sets with catch: Larvae	Percentage of sets with catch: Juveniles	Number/set: Larvae	Number/set: Juveniles	Larval/Juvenile ratio
I	6	42	0.1	1.7	0.07
II	11	50	0.2	5.7	0.03
III	44	48	1.4	24.6 (8.4)*	0.06 (0.17)*
IV	94	62	7.4	10.5	0.70
V	76	59	2.4	17.3	0.14

* Catch rate and larval/juvenile ratio if the extremely high catch (415 juveniles) of station 45 is deleted.

B

Shoreward of the HVC

Transect	Percentage with catch: Larvae	Percentage with catch: Juvenile	Number/set: Larvae	Number/set: Juvenile	Larval/Juvenile ratio
I	9	50	0.2	2.1	0.10
II	14	71	0.1	8.9	0.01
III	47	66	1.8	40.2 (12.5)*	0.04 (0.14)*
IV	100	40	10.0	16.2	0.62
V	86	50	2.7	20.7	0.13

* Catch rate and larval/juvenile ratio if the extremely high catch (415 juveniles) of station 45 is deleted.

C

HVC

Transect	Percentage with catch: Larval	Percentage with catch: Juvenile	Number/set: Larval	Number/set: Juvenile	Larval/Juvenile ratio
I	0	25	0	0.8	–
II	0	66	0	6.0	–
III	60	20	0.8	1.3	0.62
IV	88	75	4.6	7.0	0.66
V	66	66	0.7	1.3	0.54

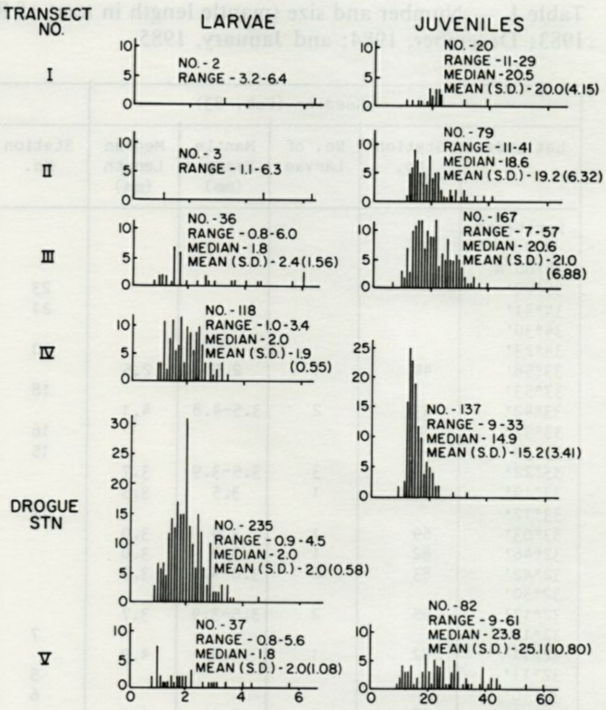


Fig. 3. — Length frequencies (mantle length in mm), range, and measures of central tendency, by transect, (see inset, Fig. 6) for larval and juvenile *Illex* for 7-22 January, 1985, cruise period.

Table III. — Number and size (mantle length in mm) of juvenile *Illex* in relation to latitude in February, 1983, and January, 1985.

	Needler (Feb. 83)								Needler (Jan. 85)			
	LEG I				LEG II							
Latitude	Station No.	No. of Juveniles	Mantle Range (mm)	Median Length (mm)	Station No.	No. of Juveniles	Mantle Range (mm)	Median Length (mm)	Transect No.	No. of Juveniles	Mantle Range (mm)	Median Length (mm)
Northeast												
37°39'N					120	2	23-30	26.5				
36°00'									I	20	11-29	20.5
34°38'	24	38	9-18	13.3								
34°30'									II	80	11-41	18.6
33°55'					84	126	14-86	32.3				
33°53'					86	3	24-43	31.0				
33°29'					70	20	16-30	23.5				
33°28'	65	7	13-27	16.0								
32°47'	82	5	21-53	24.0								
32°30'									III	~616	7-57	20.6
32°18'	95	4	19-23	19.5								
32°13'	94	15	7-30	13.0								
32°12'	92	34	7-30	10.3								
32°08'	88	4	9-13	12.5								
32°04'	107	1	29.0	29.0								
31°56'	108	1	24.0	24.0								
31°45'	114	5	44-56	47.0								
31°43'	112	5	14-24	22.0								
31°25'	122	4	11-27	22.5								
31°16'					55	4	19-76	44.5				
30°53'					45	7	20-68	43.0				
30°51'	129	5	15-37	20.0								
30°51'	131	29	13-72	31.0								
30°27'	137	359	9-66	30.9								
30°27'	139	1	36.0	36.0								
29°49'					8	4	20-51	35.0				
29°23'					16	1	22.0	22.0				
29°17'					20	64	19-92	31.5				
28°44'					31	2	32-37	34.5				
28°43'					33	13	18-35	22.3				
28°30'									IV	137	9-33	14.9
25°25'									V	~294	9-60	23.8
Southwest												

Table IV. — Percentage of stations including ommastrephids where A', B', C' Rhynchoteuthion types of larvae were caught either individually or in combination on a) Needler 1985 survey and b) Hudson 1984 survey.

		Percentage of stations with occurrence						
Transect	No of stations	A' only	B' only	C' only	A+B	A+C	B+C	A+B+C
a) Needler 85								
I	6	50	0	17	33	0	0	0
II	4	50	0	25	0	25	0	0
III	18	17	0	56	0	17	11	0
IV	28	0	0	32	0	14	36	18
V	15	0	0	20	7	27	27	13
All transects	71	13	0	33	4	17	23	10
b) Hudson 84								
All stations	16	13	6	38	6	13	31	0

Stream. On Leg II of the survey, however, catches were most frequently taken at or slightly seaward of the 15 °C isotherm, suggesting that they were principally in the High Velocity Core of the Stream. Larval catches on the Hudson 84 survey were most frequently taken at stations where the surface current was flowing at more than 1 ms^{-1} to the northeast (Fig. 5) and generally on the seaward side of the 15 °C isotherm at 200 m (Trites and Rowell, 1985). Larval and juvenile catch data for all stations of the Needler 85 survey are presented in Figure 6 with the estimated location of the High Velocity Core of the Gulf Stream. Although not clearly defined for all transects, the data suggest that highest catch levels tended to occur most frequently on the shoreward side of the High Velocity Core. To evaluate this further, catch data from each transect of the Needler 85 survey were lumped into two groups, one for all catches made shoreward of the Slope/Gulf

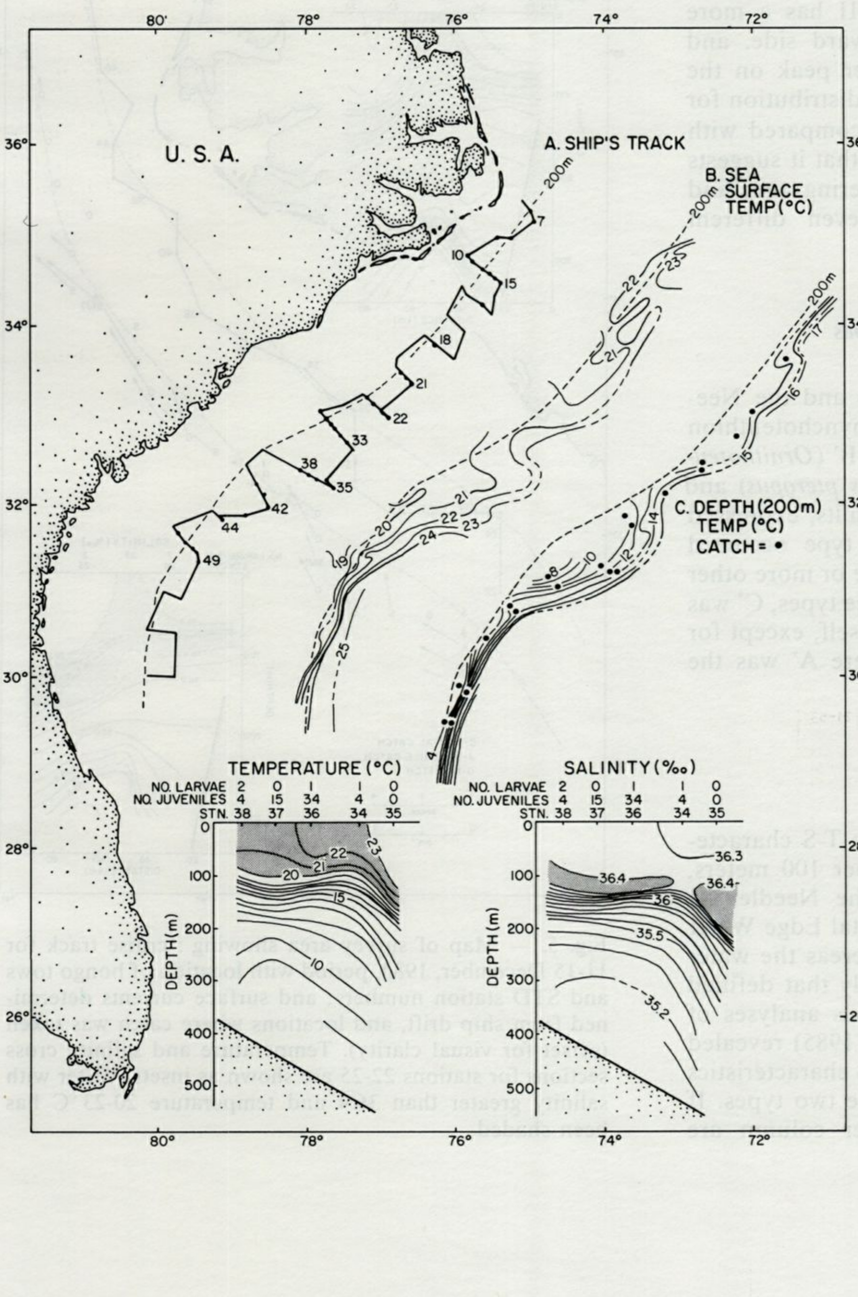


Fig. 4. — Map of survey area showing : (A) cruise track for 31 January-13 February, 1983 period with XBT's and station numbers of STD's; (B) sea surface temperature in °C; and (C) temperature at 200 m, including locations at which squid larvae and/or juveniles were caught. Figures B and C have been progressively offset for visual clarity. Temperature and salinity cross-sections for stations 34-38, off Charleston, are shown as insets. Water with salinity greater than 36.4 and temperature 20-23 °C has been shaded.

Stream Frontal Zone and the other for catches made in the High Velocity Core of the Gulf Stream (Table IIB and C). If larval catches in Transects I and II, which totalled only 5, are ignored, the percentage of stations having a catch range from moderate to high (47-100 %), with no clear pattern across the Frontal Zone. Abundance (catch/tow) of larvae is highest on Transect IV, with the shoreward catch rate twice that in the High Velocity Core. The pattern is similar for all transects. For juveniles, the percentage of stations with catch ranges from 40-71 in the shoreward side of the Frontal Zone, and from 20-75 in the High Velocity Core. Catch per tow is consistently higher in the shoreward side of the Frontal Zone by a factor ranging from 1.4 to 30.9.

Although the numbers of larvae caught in all but one transect are too small to determine size frequency distributional differences, it is clear in Transect IV that smaller larvae are concentrated shoreward of the High Velocity Core of the Gulf Stream (Fig. 7 A). For juveniles there is no clear overall pattern. However, Transect II has a more clumped distribution on the shoreward side, and Transect IV displays a much sharper peak on the shoreward side. The very broad, flat distribution for the shoreward side of Transect IV, compared with the other 4 transects is interesting in that it suggests a mixing of juveniles of widely differing ages and possibly developmental rates, or even different species of *Illex*.

Associated Rhynchoteuthion Larval Types

Samples taken on the Hudson 84 and the Needler 85 cruises were sorted for Rhynchoteuthion larval types A' (*Ommastrephes* spp.), B' (*Ornithoteuthis antillarum* and/or *Ommastrephes pteropus*) and C' (*Illex* spp.). A summary of the results, expressed as percent of stations where each type occurred separately of in combination with one or more other types, is given in Table IV. Of the three types, C' was the one most frequently present by itself, except for the two northernmost transects, where A' was the one most likely to occur by itself.

Catch in Relation to Water Masses

Rowell *et al.* (1984) found that the T-S characteristics of the water mass in the upper 100 meters, where catches were made during the Needler 83 survey, were very similar to Continental Edge Water as defined by Wennekens (1959) whereas the water further offshore matched more closely that defined as Yucatan Straits Water. Water mass analyses of Hudson 84 data (Trites and Rowell, 1985) revealed that catches were made where the T-S characteristics were generally midway between these two types. If only the upper 50 m of the water column are considered, then all Needler 83 catches were made at a temperature of approximately 22.0 ± 2.0 °C and a salinity of 36.3 ± 0.2, while the December, 1984, catches were made at a temperature of 24.0 ± 1.5 °C and salinity of 36.3 ± 0.1.

Catch in Relation to Upwelling

Physical oceanographic studies of the propagation of meanders, frontal eddies or filaments in the area between the Straits of Florida and Cape Hatteras indicate the presence of a cold dome underpinning the moving meanders (Bane *et al.*, 1981; Brooks and Bane, 1981, 1983; Lee *et al.*, 1981; Lee and Atkinson, 1983). Oceanographic sections off

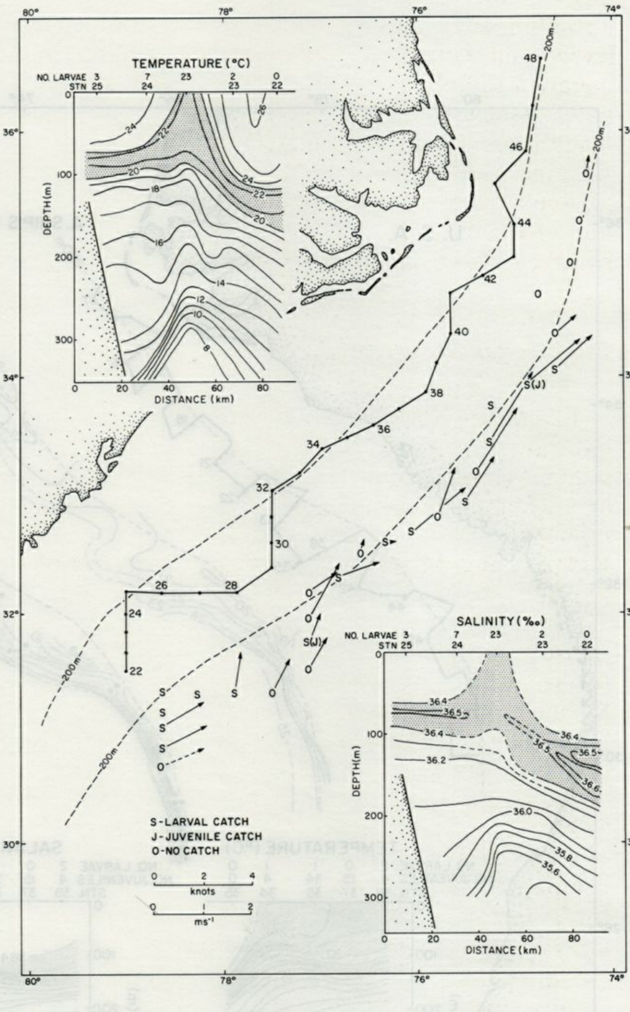


Fig. 5. — Map of survey area showing : cruise track for 11-15 December, 1984, period with location of bongo tows and STD station numbers; and surface currents determined from ship drift, and locations where catch was taken (offset for visual clarity). Temperature and salinity cross sections for stations 22-25 are shown as insets. Water with salinity greater than 36.4 and temperature 20-23 °C has been shaded.

the Charleston area, taken in the 1983, 1984, and 1985 cruises all show evidence of a cold dome on the shoreward side of the Gulf Stream (see insets, Figs. 4, 5 and 6). Although all three cruises showed relatively high larval/juvenile catches at most stations on the shoreward side of the High Velocity Core of the Gulf Stream in the Charleston area, highest concentrations occurred in or near the areas of upwelling. Lee and Atkinson (1983) concluded that the frontal eddies have considerable influence on primary production on the outer shelf. They concluded that upwelling in the cold dome, together with onshore flow in the cyclonic circulation, transports the deeper, nutrient-rich Gulf Stream waters into the euphotic zone for phytoplankton uptake. Rapid utilization of newly upwelled nutrients results in elongated patches of phytoplankton that propagate with the cold dome (Yoder *et al.,* 1981). The higher concentrations of larval *Illex* in and near upwelling areas may be associated with higher food levels and better survival rates or, alternatively, merely a sampling artifact. If larvae were preferentially associated with a particular water mass normally present only in a small deeper portion of the sampled water-column, then in upwelling areas this particular water mass occupies a much larger fraction of the column and hence a larger catch should be taken in the oblique tows (see insets, Fig. 5).

Evidence for Spawning in the Cape Canaveral Area

Examination of the larval size frequency spectra indicates that the smallest size range and nearly symmetric distribution occur in the Cape Canaveral area (Fig. 3). Examination of the larval/juvenile ratio for the 5 transects occupied between Cape Hatteras and Miami in 1985 (Table II A) indicates a value about an order of magnitude higher in Transect IV, off Cape Canaveral, than in any other transect. It is possible that a brood of larvae, hatched further south, may have been transported in the Gulf Stream and subsequently ejected out of the Stream by a Frontal Eddy in the Cape Canaveral area. However, the enormous alongstream diffusion produced by the shear in the Frontal Zone of the Gulf Stream, appears likely to diffuse larvae in a matter of a few days in the downstream direction on a scale comparable to the distance between transects, therefore, the uniqueness of Transect IV compared to III and V, supports the suggestion that a major local spawning area exists off Cape Canaveral.

Multiple Broods and Multiple Spawning Locations

The capture of recently hatched larvae on both the Hudson 84 and Needler 85 surveys indicates that spawning spans many weeks. Likewise, the presence of newly hatched larvae, less than 1 mm ML, and juveniles, greater than 60 mm ML, in the same area and time (e.g., Transect V, Fig. 3) indicates a relatively protracted spawning period. Although the extent to which spawning occurs as a series of "events", each concentrated over a short period of time, is unknown;, some of the size frequency diagrams (Figs. 3 and 7) do show more than one peak, suggesting a multiple brood composition. The possibility also exists, particularly in the more southern transects, that more than one species is involved.

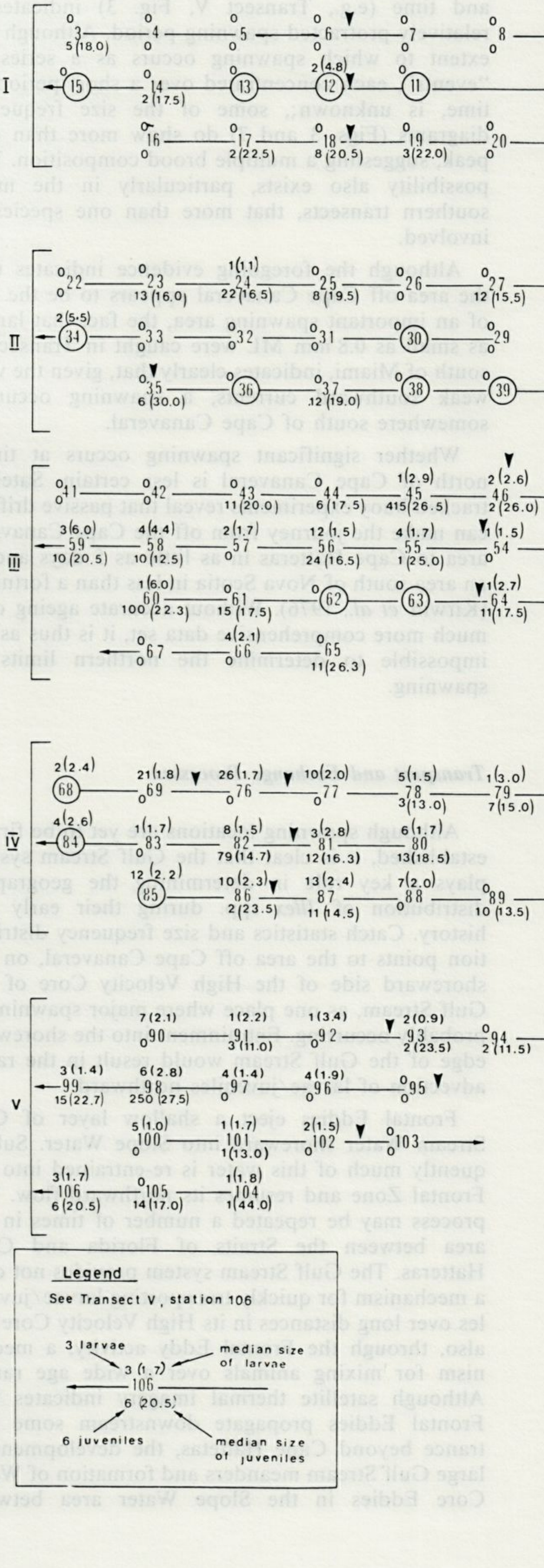
Although the foregoing evidence indicates that the area off Cape Canaveral appears to be the site of an important spawning area, the fact that larvae as small as 0.8 mm ML were caught in Transect V, south of Miami, indicates clearly that, given the very weak southward currents, a spawning occurred somewhere south of Cape Canaveral.

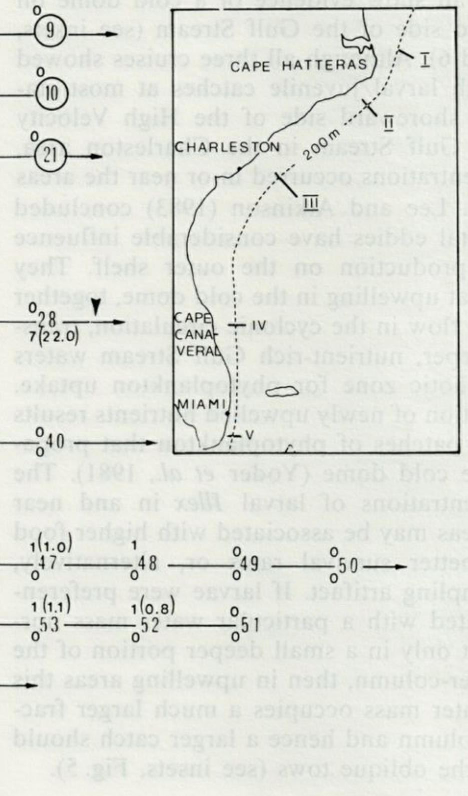
Whether significant spawning occurs at times north of Cape Canaveral is less certain. Satellite tracked buoy experiments reveal that passive drifters can make the journey from off the Cape Canaveral area to Cape Hatteras in as little as 5 days and to an area south of Nova Scotia in less than a fortnight (Kirwin *et al.,* 1976). Without accurate ageing or a much more comprehensive data set, it is thus as yet impossible to determine the northern limits of spawning.

Transport and Exchange Processes

Although spawning locations are yet to be firmly established, it is cleat that the Gulf Stream system plays a key role in determining the geographic distribution of *Illex* spp. during their early life history. Catch statistics and size frequency distribution points to the area off Cape Canaveral, on the shoreward side of the High Velocity Core of the Gulf Stream, as one place where major spawning is probably occurring. Entrainment into the shoreward edge of the Gulf Stream would result in the rapid advection of larvae/juveniles northward.

Frontal Eddies eject a shallow layer of Gulf Stream Water shoreward into Slope Water. Subsequently much of this water is re-entrained into the Frontal Zone and resumes its northward flow. The process may be repeated a number of times in the area between the Straits of Florida and Cape Hatteras. The Gulf Stream system provides not only a mechanism for quickly transporting larvae/juveniles over long distances in its High Velocity Core but also, through the Frontal Eddy activity, a mechanism for mixing animals over a wide age range. Although satellite thermal imagery indicates that Frontal Eddies propagate downstream some distrance beyond Cape Hattetas, the development of large Gulf Stream meanders and formation of Warm Core Eddies in the Slope Water area between


I
II
III
IV
V
Legend
See Transect V, station 106
3 larvae
median size of larvae
6 juveniles
median size juveniles


CAPE HATTERAS
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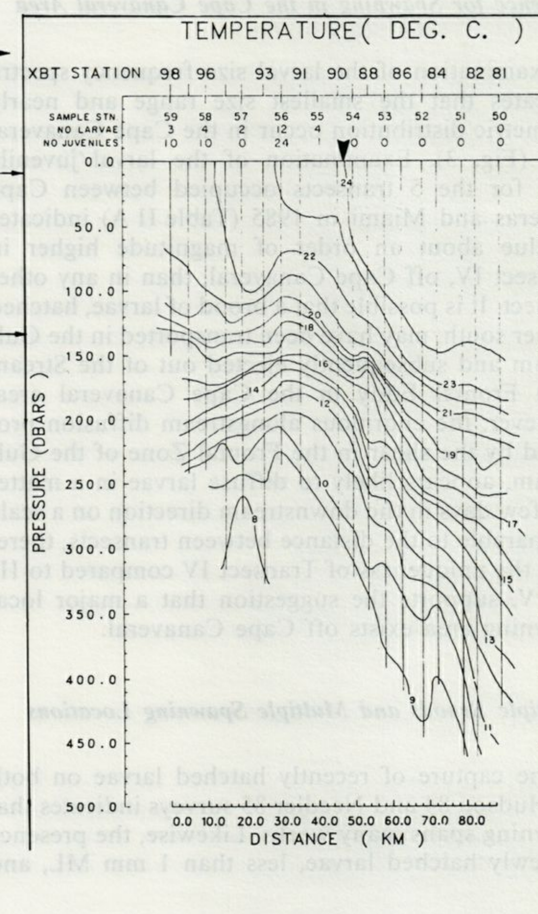
TEMPERATURE(DEG. C.)
XBT STATION
SAMPLE STN
NO LARVAE
NO JUVENILES
PRESSURE (DBARS)
DISTANCE (KM)

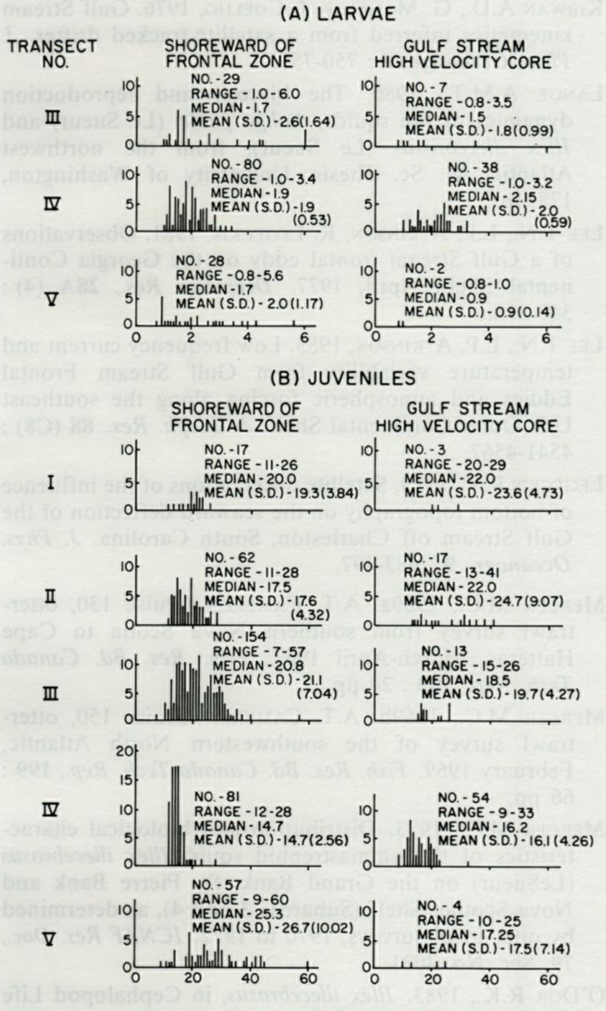

Fig. 7. — Length frequencies (mantle length in mm), range and measures of central tendency for larval captures (A) and juvenile captures (B) at grouped stations shoreward of Frontal Zone and in High Velocity Core of Gulf Stream, by transect (see inset, Fig. 6) for 7-22 January 1985 cruise period.

50-70 °W, provide a mechanism for transporting large volumes of larval/juvenile bearing water shoreward (Trites, 1983). Since Warm Core Eddy dimensions are typically 200-300 km in diameter and have a mean life span of 3-4 months (Trites and Drinkwater, 1985), they provide a mechanism potentially capable of removing large numbers of larvae/juveniles from the Gulf Stream and facilitate their subsequent migration onto the Continental Shelf between Newfoundland and Cape Cod.

Summary

1. Larvae and early juveniles are caught mainly in a narrow but very long strip of water centered in the Slope Water/Gulf Stream Frontal Zone extending from Florida to and beyond Cape Hatteras.

2. Both the Needler 83 and 85 data show more than one peak in the size frequency distributions suggesting that a sequence of brood hatching occurs.

3. A larval to juvenile catch ratio on a transect in the Cape Canaveral area on the Needler 85 survey, compared to transects to the north and south of it, together with the presence of very small larvae, and the more "compact" character of the length frequency distribution suggest that this may be near a major spawning area.

4. The presence of newly hatched larvae south of Miami, indicates that spawning also occurs south of the Cape Canaveral area.

5. The physical environment is probably a major factor determing larval/juvenile distribution in that : (a) The Gulf Stream provides a rapid transport system (as much as 1000 km/week). (b) Frontal Eddies eject surface-layer Gulf Stream Water shoreward into Slope Water, which is subsequently re-entrained into the Stream. (c) Frontal Eddies produce upwelling of nutrient-rich water between the filament and the Gulf Stream proper, which in turn increases primary production in the Slope/Gulf Stream Frontal Zone. (d) Downstream from Cape Hatteras the formation of Warm-Core Gulf Stream Eddies eject large quantities of Gulf Stream Water into the Slope Water area south of Nova Scotia and the Grand Banks with eddy duration times typically of several months.

6. Higher catches in the upwelling zone may be : (a) The result of passive advection. (b) Related to increased availability of food and hence better survival rates. (c) A sampling artifact.

7. Recruitment success or failure may be critically dependent on the timing, location and number of Gulf Stream Frontal Eddies and Warm Core Eddies developing when larvae and/or juveniles are present.

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Fig. 6. — Larval and juvenile *Illex* catch taken on repeated occupation of stations along five transects (see inset for locations) during cruise period 7-22 January, 1985. Number of larvae, juveniles, and their median mantle length (mm) are shown at each sampling station. Temperature cross-section, taken during second occupation of Transect III, together with number of larvae and juveniles caught at each sampling station are shown in an inset. Vertical arrowhead denotes estimated location of High Velocity Core of Gulf Stream.

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