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Life history strategies of the squid, *Illex illecebrosus*, in the Northwest Atlantic

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Abstract

Time series (1965-1985) of *Illex illecebrosus* catch and morphometric data from the Northwest Atlantic were analysed to describe geographic variability in population structure. The areas studied were NAFO sub-areas 3 to 6, which range from Newfoundland to the northeastern USA shelf. Population components, reflecting seasonal spawning groups, were identified based on analysis of length frequency data. Components 3 and 4 represent two prominent life cycles: the summer spawners and winter spawners respectively. Components 1, 2, and 5 do not represent different life cycles, but result from the capacity to shift between life cycles by prolonging (or shortening) the life span. The presence of up to five components in the southern area illustrates a life history strategy involving protracted spawning and complex population structure. There was clear geographic variability in annual catch, with fluctuations being most extreme in the most northern area. Annual catch levels in all areas were significantly correlated with the abundance of the winter-spawning component, as represented by the number of squid within samples which belong to component 4. Population structure in the most northern area was simplest and catch levels therefore were most dependent on the highly migratory winter-spawning component. This leads to greater catch variability in the most northern area than in the other areas. The advantages of good feeding conditions may compensate for the risks associated with long-range migrations, especially recruitment failure. Life history strategies involving migratory and non-migratory population components limit the risk of recruitment failure. The overall resultant life history strategy for *Illex illecebrosus* is one that ensures survival of the species by stabilizing recruitment in at least one (southern) area through protracted spawning, complex population structure and interaction of spawning components.

Keywords: Cephalopoda, squid, catch, population structure, life history strategies, life cycles, Atlantic.

Les adaptations du cycle biologique du calmar, Illex illecebrosus, *dans l'Atlantique nord-est.*

Résumé

Des séries temporelles (1965-1985) de captures et de données morphométriques d'*Illex illecebrosus* de l'Atlantique nord-est sont analysées afin de décrire les variabilités géographiques de la structure de la population. Les zones de pêche (NAFO) sont les sous-divisions 3 à 6, qui s'étendent de Terre-Neuve au plateau continental nord-est des Etats-Unis. Les composantes de la population, reflétant des groupes saisonniers de reproduction, sont identifiées au moyen d'analyses de fréquence de taille. Les composantes (classes de taille) 3 et 4 correspondent respectivement aux reproducteurs estivaux et hivernaux représentant 2 principaux types de cycle biologique. Les composantes 1, 2 et 5 ne représentent pas plusieurs cycles biologiques, mais résultent de la capacité de décalage entre les cycles par prolongation ou raccourcissement de la durée de vie. La présence de plusieurs composantes, jusqu'à cinq dans la zone sud, illustre une stratégie comportant une période de reproduction prolongée et une structure complexe de la population. Il existe une variabilité géographique évidente dans les captures annuelles, les fluctuations les plus fortes

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s'observant dans le nord de la zone. Les niveaux de captures annuelles de toutes les zones sont corrélés de façon significative avec la composante de l'abondance des reproducteurs hivernaux, représentée par le nombre de calmars de l'échantillon qui appartiennent à la composante n° 4. La structure de la population du nord de la zone était la plus simple, ce qui rend les niveaux de capture dépendants de l'importance de la migration de reproduction hivernale. Ceci entraîne une plus forte variabilité des captures dans la zone la plus septentrionale que dans les autres zones. Les avantages procurés par de bonnes conditions trophiques peuvent compenser les risques associés à des migrations de grande envergure, en particulier une baisse du recrutement. Des adaptations du cycle biologique, mettant en jeu des populations migratoires et non-migratoires, limitent les risques de chute du recrutement. La stratégie globale de vie d'*Illex illecebrosus* assure la survie de l'espèce en stabilisant le recrutement, au moins dans la zone sud grâce à un allongement de la période de reproduction et d'une structure complexe de la population.

Mots-clés : Céphalopode, calmar, capture, structure de la population, cycle de vie.

INTRODUCTION

The ommastrephid squid, *Illex illecebrosus*, is semelparous with a one-year life expectancy and has a wide geographic range of distribution along the coast of North America. Data on larval distribution (Dawe and Beck, 1985; Hatanaka *et al.*, 1985; Rowell *et al.*, 1985), oceanographic regime (Trites, 1983) and migration of adults (Dawe *et al.*, 1981) indicate that this species has the capacity to undertake extensive migrations between the low latitudes of Southern USA and the high latitude of Eastern Canada. Fishery statistics have shown that area-specific abundance of *Illex illecebrosus* becomes progressively irregular from regions of low to high latitude (Coelho, 1986). The southern portion of the population is stabilized at moderate levels and may be limited by competition for food (E. G. Dawe and J. Brodziak, pers. comm.). The northern portion can be substantial in some years perhaps due to a large food resource, but in other years the population is minimal because of poor recruitment of juveniles.

Recruitment is likely to be at least partially dependent on successful spawning conditions. Spawning may be limited to sea-water temperatures greater than 12.5°C, based on requirements for successful embryonic development (O'Dor *et al.*, 1982). On this basis, spawning during winter may be restricted to the southern portion of the continental shelf, south of Cape Hatteras to Chesapeake Bay, although suitable temperatures exist along the continental slope during winter at least as far north as 40°N (Trites, 1983). However, during the summer, the area on the continental shelf that is suitable for embryonic development extends northward (Trites, 1983). The northern portion of the *Illex illecebrosus* population is dependent on the successful dispersal of eggs and larvae, from the south, as well as shoreward migration of juveniles. The extent of dispersal and migration may be affected by environmental variation (Dawe and Warren, 1992), perhaps due to effects of such variation on mechanisms of initial transport, within the Gulf Stream Frontal Zone (Trites, 1983; A. Bakum and J. Csirke, pers. comm.).

In this paper, morphometric data were collected from three fishery areas to determine a population pattern based on size and component. Component refers to a group of squid spawning at a specific time, given that winter –and summer– spawning peaks within a protracted spawning period are known for this species (Lange and Sissenwine, 1983; Coelho, 1986; Coelho and O'Dor, 1993). Geographic variability in population structure is investigated. Furthermore, possible relationships between population structure and the annual catch are investigated. Life history strategies and ecological principles which are related to the severe catch fluctuations and the occasional virtual absence of squid in the northern-most areas are discussed.

METHODS

This study includes a re-analysis of data collected in the Northwest Atlantic Fisheries Organization (NAFO) area designated as sub-area 3 (*table* 1) (Coelho, 1986). Also, a time series of length data was provided for NAFO sub-area 4 (*table* 2) (Mohn, 1981) and for NAFO sub-areas 5 + 6 (*table* 3) (A.M.T. Lange, pers. comm.). Sampling ranged from 1970 to 1985 for sub-areas 4 and 5+6, and from 1965 to 1982 for sub-area 3. Sub-areas 3 and 4 correspond respectively to inshore Newfoundland and the Nova Scotian Shelf. Sub-area 5 + 6 represents the northeastern USA shelf (*fig.* 1). Sampling procedure and time of sampling varied among areas. Sampling on the continental shelf was generally part of groundfish bottom trawl surveys carried out during September to October on the northeastern USA shelf and during July on the Scotian Shelf. Sampling at inshore Newfoundland varied throughout July to November and was by jigging.

The Bhattacharya method (Bhattacharya, 1967) was used to treat the length frequency data in those cases where multimodality suggested that the population consisted of several components. The LFSA (Length based Fish Stock Assessment) package of microcomputer programs was used to apply the Bhattacharya method (Sparre, 1987). This method

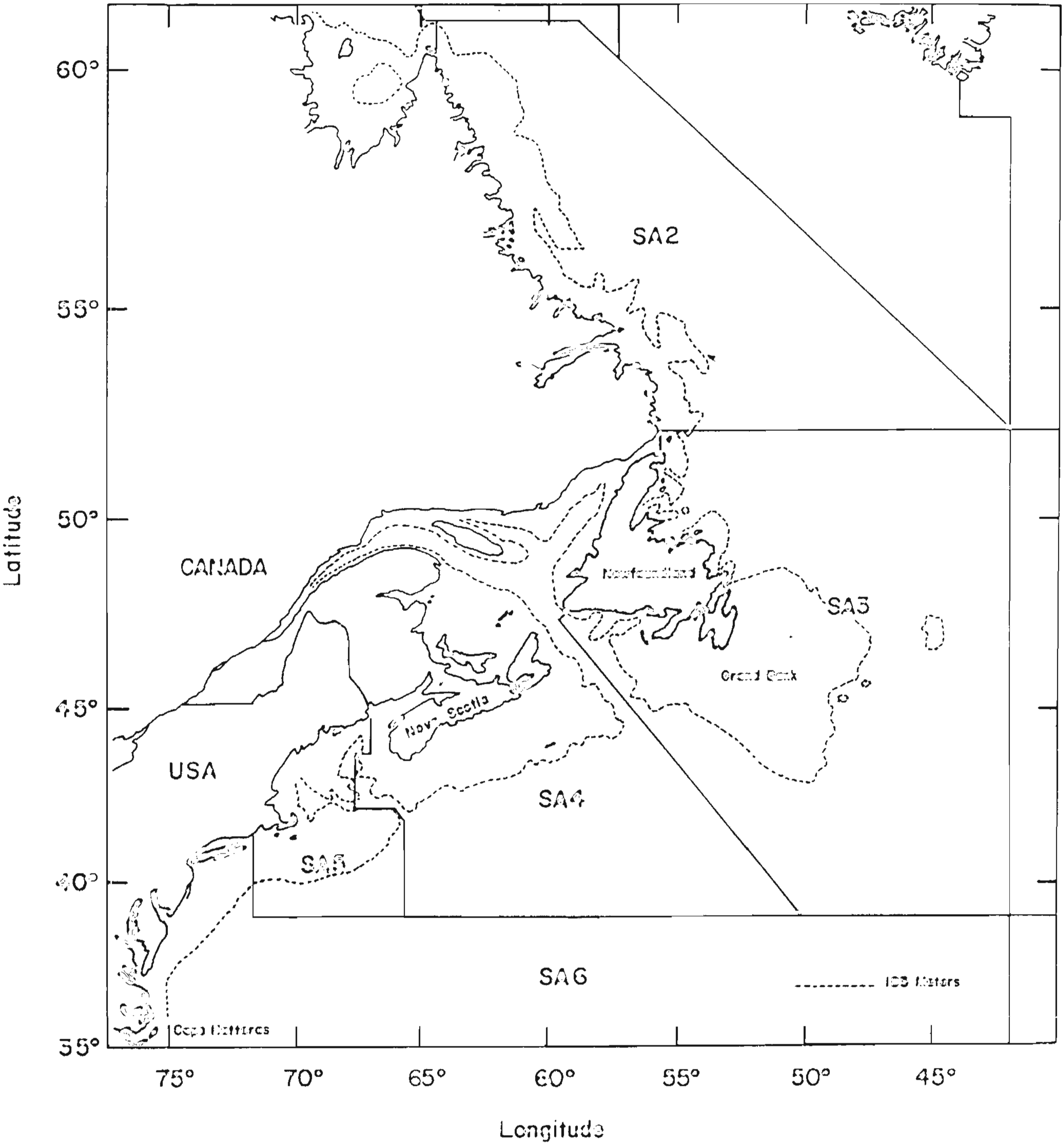

Figure 1. – The fishing areas of the Northwest Atlantic Fisheries Organization, including the major areas of the squid *Illex illecebrosus* fishery; Sub-areas 3, 4, 5 and 6.

consists basically of separating normal distributions, each representing a component of the sampled population, from the overall distribution on the left-hand side of the total distribution. The whole process can be divided into the following steps (Sparre *et al.*, 1989):

a) Determine an uncontaminated (clean) slope of a normal distribution on the left side of the total

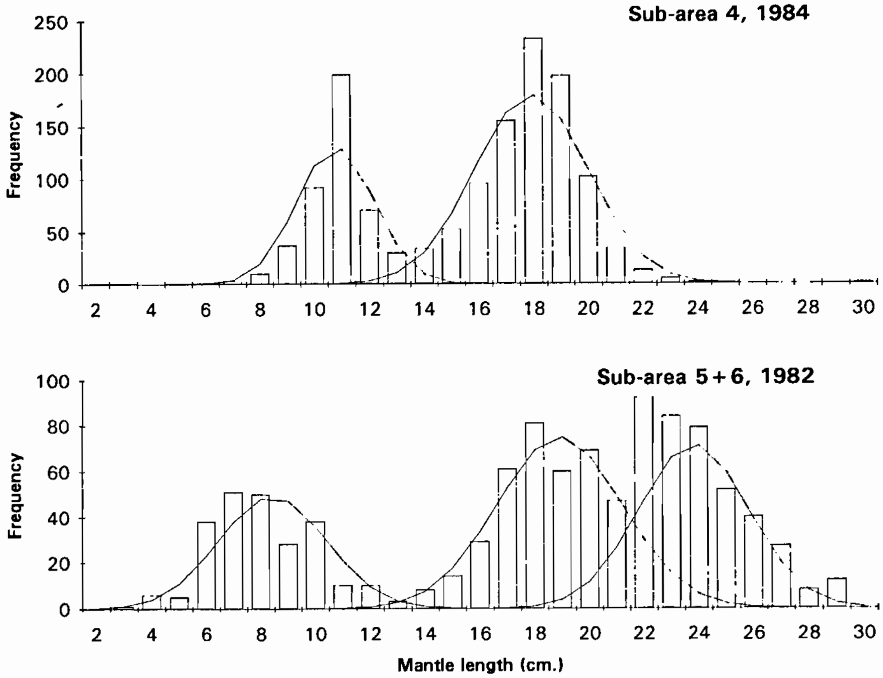

Figure 2. – Observed length frequency (histogram) and estimated normal distributions (curves) for sub-area 4 (offshore Nova Scotia) in 1984 and sub-area 5 + 6 (offshore USA) in 1982. Component separation indices are 4.095 in 1984 for sub-area 4, and 4.942 and 2.295 for successive components in 1982 for sub-area 5 + 6.

distribution;

b) Determine the normal distribution of the first component by means of a transformation into a straight line;

c) Determine the numbers of squid (in this case) per length group belonging to that first component and then subtract them from the total distribution;

d) Repeat the process for the next normal distribution from the left, until no more clean normal distributions can be found.

Examples of the observed length frequency distribution and estimated normal distributions according to the Bhattacharya method are presented in *figure* 2.

It can be very difficult to assess whether the estimated normal distributions are reasonable as compared to the total distribution. A "separation index" was used as a criterion for evaluating the estimated normal distributions (Sparre *et al.*, 1989). If the separation index I is less than two it is virtually impossible to separate the components.

Identification and designation of components, based on length frequency distributions, was performed separately for each area because of the great area diferences in sampling regime. Therefore mean mantle length for any component would be expected to vary considerably among areas. Since most components were found in sub-area 5 + 6, designation started with these data and involved the following steps:

a) Components with mean mantle lengths found in the intervals 5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, and 25 cm – were designated 1 to 5, respectively;

b) The same procedure was applied to sub-area 3;

c) The same procedure was applied to sub-area 4. Thereafter the original component designation was increased by one in this area.

Adjustment is necessary when two means of a particular year were in the same interval. The mean nearest the limits of the interval was moved. Step C was an attempt to avoid mis-assignment of components in sub-area 4, which were generally characterized by smaller mean mantle lengths. It is assumed that this was due to the earlier sampling time in comparison to the other areas.

There are some very basic assumptions that should be stated at this point regarding the treatment of data. Although it was not possible to standardize the sampling times and gear among areas, it is assumed that the data reflect the abundance of a particular size of squid. Given the rate that this annual species grows, the pooling of several months data from inshore Newfoundland may be expected to blurr the separation of components. This is true to a certain extent, but sampling generally occurred during a restricted time of year (late summer and autumn), so pooling of data is assumed to be justified. The resulting error due to this procedure was taken into account by not attempting to estimate actual length characteristics of components. It was rather a comparison of patterns among areas.

After component designation, possible relations between population structure and the annual catch were investigated. Correlation coefficients were calculated between annual catch and the sampled abundance of the dominant components. The Kendall correlation procedure (SAS, 1988) was utilized, since the methods applied to component identification and designation do not meet parametric conditions.

RESULTS

Population structure

Results of the Bhattacharya analysis and the subsequent component designation are presented in *tables* 1 to 3. Component designation by intervals resulted in a consistent pattern, characterized by a low variation of the modal lengths for the recurring components 3 and 4.

Table 4 presents the mean mantle lengths which are essentially a calculation of means weighted by the frequency of observations in each length interval. Separation of components from the total length frequency distributions was carried out if the "separation index" exceeded 2, as stated in the methods.

Table 4 shows that only three components were observed in sub-areas 3 and 4, while five components were observed in sub-area 5 + 6. In sub-area 3 they were components 3 to 5, components 2 to 4 in sub-area 4, and components 1 to 5 in sub-area 5 + 6. Common to all areas were components 3 and 4, component 4 being the most abundant in all areas. Component 3 was also relatively abundant in sub-area 3.

Three to four components were often observed in sub-area 5 + 6 in contrast to sub-areas 3 and 4, where one or two components were most common (*table* 5). Length data reflected a rather complex population structure in sub-area 5 + 6, the southern area of this study, in comparison to sub-areas 3 and 4. Both the overall means data and the yearly number of components present in the population reflected the more complex population structure in the most southern area.

Variability of the fishery catch

This section deals with possible relationships between population structure and annual catch. *Figure* 3 illustrates the variability, particularly in the northern sub-area 3, of the annual catch during the period of this study. The coefficient of variation of the annual catch further illustrates this point in that it was 42% in sub-area 5 + 6, 120% in sub-area 4, and 155% in sub-area 3. It is assumed that catch fluctuations were not caused by varying fishing effort, but actually reflected abundance.

The numbers of squid of components 3 and 4 within samples were chosen as good indicators of population structure, since these components dominated the samples and were found in all areas (*table* 5). Kendall correlation coefficients were calculated between annual catch and number of squid of these components within samples. Possible correlations among components were also taken into account.

There was a significant correlation between number of component 4 squid sampled and annual catch for all areas; Pr > R: 0.04, 0.02, and 0.01 for sub-areas 3, 4, and 5 + 6, respectively (n = 15 in each case). *Figure* 4 illustrates the tendency for increasing annual catch with increasing number of component 4 squid, although there was great variation.

There was also a highly significant correlation between number of component 4 squid sampled and total squid sampled for all areas; Pr > R: 0.001, 0.001, and 0.006 for sub-areas 3, 4, and 5 + 6, respectively. Since component 4 squid generally dominated the samples, their abundance was reflected in the total sampled. It would therefore seem difficult to determine whether the fluctuations in the catch were in fact correlated to the component 4 squid in particular, and not the total squid sampled.

Since the correlations between total squid sampled and annual catch in sub-areas 3 and 4 were not significant (Pr > R: 0.22 and 0.05, respectively), catch therefore appears to be related to the productivity of component 4, in particular, in the most northern area.

In sub-area 5 + 6, the total squid sampled was significantly correlated to the annual catch (Pr > R: 0.03), which further underlines the more complex relationship between population structure and annual catch in the most southern area than in the more northern areas. The correlation of annual catch with component 4 (Pr > R: 0.01) was nevertheless stronger than that with total sampled in this sub-area also (Pr > R: 0.03), again stressing the importance of component 4 in affecting catch.

The significant correlations between annual catch and component 4 do not therefore simply reflect the collection of large samples of squid (of all components including component 4) when total population abundance is high. It is also important to note that the difference in correlations of annual catch with component 4 versus with total squid is greatest at the most northern area and smallest at the most southern area, indicating that dependence of annual catch on abundance of component 4 increases from south to north.

There was no significant correlation in all areas between annual catch and number of component 3 squid (Pr > R: 0.60, 0.91, 0.88 for sub-areas 3, 4, 5 + 6, respectively). In sub-areas 4 and 5 + 6 there was no significant correlation between components 3 and 4 (Pr > R: 0.08 and 0.17, respectively), which suggests that these components followed a different cycle of abundance in the most southern area. Only in the most northern sub-area 3 did a significant correlation between components 3 and 4 occur (Pr > R: 0.04),

Table 1. – Length frequency data for sub-area 3 (inshore Newfoundland). Symbols indicate the mode of each estimated component, following the Bhattacharya analysis and a designation by interval including all areas (see methods); open star-comp. 3; solid star-comp. 4; solid circle-comp. 5. Components 1 and 2 (smaller squid) were not found in this area. Notice lack of samples in years of very low catches in the fishery; 1968, 1972, 1974.

Mantle length	Year														
Lower Limit (cm)	1965	1966	1967	1969	1970	1971	1973	1975	1976	1977	1978	1979	1980	1981	1982
9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	–	–	1	–	1	1	–	–	–	–	–	–	–	–	–
12	10	2	1	–	–	1	–	–	–	–	–	–	–	–	–
13	29	26	17	–	–	11	–	–	–	–	–	–	–	–	–
14	52	127	89	–	1	17	1	–	–	–	5	5	–	–	19
15	119	385	286	–	5	116	4	–	–	–	66	20	4	19	41
16	206	782	581	–	15	325	27	–	–	1	269	131	38	109	195
17	* 247	1 090	1 012	–	22	607	136	–	–	1	476	393	104	472	752
18	257	* 1 500	* 1 231	8	99	* 718	203	–	–	7	* 716	* 460	* 178	1 256	* 977
19	335	1 783	1 221	23	286	749	263	5	2	25	942	541	500	2 244	872
20	685	1 572	1 335	92	★ 341	734	★ 266	12	12	35	1 466	782	964	★ 2 302	760
21	★ 863	1 427	1 388	106	134	924	228	62	81	★ 58	2 180	1 220	★ 1 320	1 839	489
22	612	★ 1 049	1 111	★ 100	80	★ 668	207	170	★ 162	36	★ 1 938	★ 1 434	1 126	1 041	703
23	378	724	★ 967	83	33	370	103	★ 265	164	36	1 246	1 203	826	592	★ 983
24	205	466	939	26	20	210	28	213	146	15	592	866	○ 577	323	909
25	○ 132	307	644	7	9	96	10	138	○ 113	13	270	467	341	○ 162	584
26	74	172	406	1	3	82	–	○ 110	91	○ 11	96	247	192	94	308
27	47	88	361	–	1	47	–	43	82	4	54	113	94	21	150
28	20	62	195	–	–	17	–	28	42	2	11	23	42	8	68
29	3	20	72	–	–	12	–	7	24	–	7	8	13	3	105
30	1	4	31	–	–	4	–.	3	4	–	1	4	5	–	10
31	–	2	9	–	–	–	–	1	2	–	1	1	1	–	1
32	1	1	–	–	–	–	–	–	–	1	–	–	–	–	–
33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	4 277	11 589	11 897	446	1 050	5 709	1 481	1 057	925	245	10 336	7 918	6 325	10 485	7 926

Table 2. – Length frequency data for sub-area 4 (offshore Nova Scotia). Symbols indicate the mode of each estimated component, following the Bhattacharya analysis and a designation by interval including all areas (see methods); snowflake-comp. 2; open star-comp. 3; solid star-comp. 4.

Mantle length Lower Limit (cm)	Year															
	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
4	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
5	2	1	1	–	–	3	–	–	–	–	–	–	–	4	–	1
6	2	3	–	–	–	–	–	–	–	–	–	–	4	3	–	1
7	6	* 3	–	–	–	2	1	–	–	–	–	–	8	23	3	9
8	* 11	2	–	–	1	4	–	–	–	1	1	–	23	108	10	97
9	7	3	1	–	3	* 4	–	–	1	1	2	–	* 25	252	37	298
10	2	4	1	–	1	8	1	–	5	1	–	–	15	* 247	92	* 294
11	28	6	2	–	2	7	–	–	7	7	3	2	12	168	* 199	141
12	61	15	11	2	3	1	1	–	18	29	3	1	9	183	71	46
13	* 75	25	24	5	8	4	–	3	* 18	44	23	13	40	* 151	30	25
14	72	63	62	20	27	27	7	17	24	* 46	71	52	76	115	34	67
15	117	174	123	* 33	63	50	7	31	40	45	114	96	115	54	53	127
16	★ 136	250	230	64	140	157	35	74	109	66	221	233	★ 147	18	96	★ 226
17	124	★ 305	★ 235	89	222	427	204	226	270	230	★ 288	522	177	9	155	223
18	55	322	223	174	366	★ 439	744	545	★ 603	550	278	★ 729	124	7	★ 233	128
19	30	192	129	★ 200	★ 397	274	1 488	925	436	★ 910	161	814	56	5	198	36
20	15	80	64	120	263	136	2 158	★ 831	★213	838	73	441	16	–	102	15
21	3	19	24	59	148	49	★ 1 864	550	86	347	21	203	5	–	34	4
22	–	5	–	14	101	16	1 243	346	32	175	11	45	3	–	13	6
23	2	–	–	5	66	8	601	149	11	68	3	19	1	–	5	1
24	1	–	1	2	29	–	219	70	6	14	1	5	–	–	2	1
25	1	–	–	1	6	–	67	32	1	9	1	2	–	–	1	1
26	–	–	–	1	7	–	30	16	–	3	1	–	–	–	–	2
27	–	–	–	1	1	–	2	8	–	1	1	–	–	1	–	–
28	–	1	–	3	1	1	2	2	–	1	3	–	–	–	–	–
29	–	–	–	–	–	1	–	4	–	2	–	–	–	–	–	–
30	–	–	–	–	–	–	–	3	–	–	–	–	–	–	1	–
31	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Total	750	1 433	1 187	793	1 855	1 618	8 675	3 832	1 880	3 388	1 280	3 177	856	1 348	1 369	1 749

Table 3. – Length frequency data for sub-area 5 + 6 (offshore USA). Symbols indicate the mode of each estimated component, following the Bhattacharya analysis and a designation by interval including all areas (see methods); open circle-comp. 1; snowflake-comp. 2; open star-comp. 3; solid star-comp. 4; solid circle-comp. 5.

Mantle length Lower Limit (cm)	Year															
	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	–	–	–	–	–	–	–	–	–	–	–	–	–	18	–	–
3	–	–	1	–	–	9	–	–	–	–	1	–	1	4	–	–
4	1	–	31	–	–	16	–	–	2	–	1	–	6	1	1	2
5	4	–	○ 72	–	3	91	1	1	28	1	2	–	5	3	3	1
6	48	1	21	1	5	144	5	2	○ 44	12	2	–	38	1	7	3
7	○ 146	–	7	–	3	164	–	9	16	28	5	3	51	–	○ 12	15
8	84	1	14	–	9	308	2	20	40	112	13	7	* 50	3	9	15
9	29	3	* 20	–	10	* 244	3	* 19	78	* 235	* 25	9	28	18	11	26
10	19	3	17	5	* 14	279	3	16	185	207	19	23	38	1	27	* 21
11	* 21	3	13	4	9	295	5	9	* 145	97	51	36	10	* 7	35	25
12	16	9	32	6	7	221	3	8	154	23	81	* 87	10	22	47	10
13	12	* 11	33	9	3	87	4	9	114	19	145	50	3	19	70	19
14	* 31	8	48	* 9	7	23	2	* 12	118	12	143	35	8	3	91	18
15	20	17	* 37	12	* 5	21	4	5	150	7	121	28	14	8	111	22
16	9	19	43	4	5	14	3	19	223	7	* 152	25	29	22	149	50
17	17	19	28	15	3	12	7	21	* 220	10	117	30	61	8	* 156	52
18	19	30	37	20	4	19	14	22	255	12	129	34	81	23	122	65
19	17	25	19	19	14	16	139	37	306	55	88	41	* 60	9	102	* 78
20	24	56	29	43	41	36	363	124	558	246	125	51	69	★ 20	58	89
21	32	★ 48	30	48	47	50	527	297	866	889	189	157	47	27	41	50
22	★ 33	41	★ 31	★ 64	69	77	683	433	1 314	1 469	333	335	92	13	31	33
23	23	27	15	24	70	★ 89	★ 634	465	★ 1 446	★ 1 383	360	630	84	10	14	26
24	9	33	16	36	★ 63	102	502	★ 379	1 186	916	★ 276	★ 666	★ 79	10	10	12
25	10	21	10	15	95	71	492	370	958	744	202	636	52	6	3	13
26	7	14	3	7	51	54	456	292	593	765	204	401	40	8	2	5
27	5	11	5	3	32	58	302	230	381	○ 719	157	357	27	2	–	4
28	2	9	3	11	18	46	104	154	227	483	93	○ 289	8	1	–	1
29	–	3	2	2	4	25	36	86	135	207	54	220	12	–	–	–
30	1	1	2	5	8	8	4	35	124	59	24	96	–	–	–	–
31	–	1	1	–	1	4	4	15	22	18	8	26	–	–	–	1
32	–	–	–	–	1	1	–	8	1	1	–	3	–	–	–	–
33	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–
34	–	–	–	–	–	–	–	1	1	2	–	2	–	–	–	–
35	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
37	–	–	–	–	–	–	3	–	19	–	–	–	–	–	–	–
Total	639	414	620	362	601	2 584	4 305	3 098	9 910	8 739	3 121	4 278	1 003	267	1 112	656

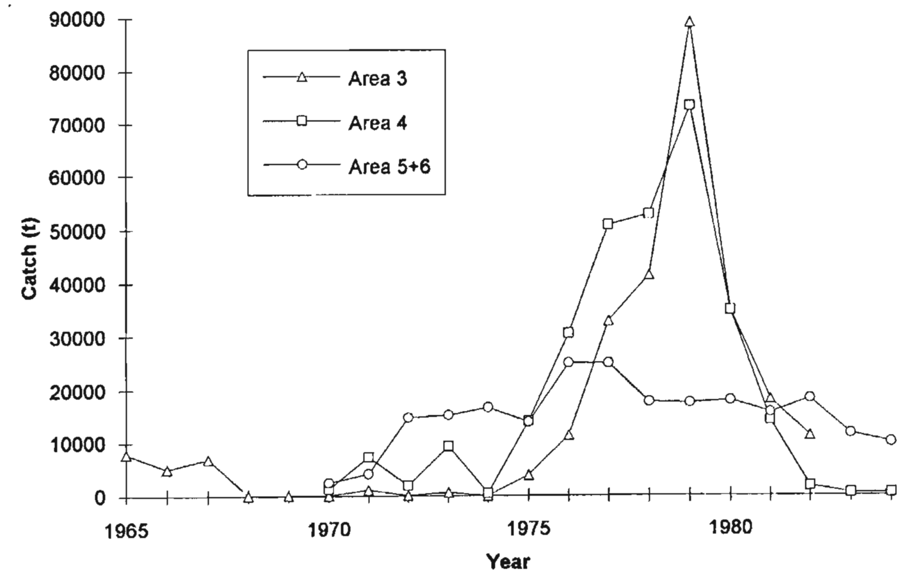

Figure 3. – Annual nominal catch (metric tons) of *Illex illecebrosus* by fishery area (Amaratunga, 1981; NAFO, 1985).

Table 4. – Mean mantle length by area and component. Calculated by including data from all sampled years.

Area	Component	Frequency	Mantle length (cm)	Standard deviation	Minimum (cm)	Maximum (cm)
3	3	26 205	18.8	0.26	18.0	19.0
3	4	50 923	22.3	1.23	20.4	24.0
3	5	4 269	25.0	0.65	24.5	26.7
4	2	2 380	10.4	0.54	7.3	11.3
4	3	1 231	13.8	0.64	13.2	15.6
4	4	31 450	19.4	1.31	16.8	20.9
5	1	569	7.1	1.04	5.4	7.9
5	2	4 336	10.2	1.01	8.9	12.6
5	3	4 860	17.1	1.27	13.8	19.4
5	4	28 980	23.9	0.71	20.5	24.8
5	5	3 200	27.7	0.57	27.4	28.7

suggesting a similar cycle of abundance between those two components.

DISCUSSION

Some difficulties were encountered in the treatment of data in this study. Sampling procedure and time of sampling varied among areas. Abundance was described using the variable number of squid sampled belonging to a certain component, and the annual catch was assumed to fluctuate independent of effort. Growth rates were assumed to be constant and similar among areas. This approach was justified by the broad objectives of this study, *i.e.* geographic variability in population structure and its relationship to the annual catch.

The failure to take sampling time or sex into consideration could have led to separation of false components, but the pooling of data over several months in sub-area 3 did not lead to the distinction of comparatively more components. Distinction of several components in sub-area 4 was possible despite sampling being limited to one month (July). Also, Coelho (1986) investigated component structure for males in sub-area 3 and found three distinct components as in this study. These observations suggest that a pooling of data did not lead to the separation of false components.

The Bhattacharya method is not a rigorous statistical method despite the helpful "separation index". Despite the element of subjectivity involved, components were easily classified by mantle length interval. As mentioned before it was considered necessary to adjust component designations in sub-area 4 to avoid misassigning components. The abundance of component 4 was consistently the highest in all areas, which indicates that component designation was successful. Another indication of correct assignment was the significant positive correlation between annual catch and the number of component 4 squid sampled in all areas, in contrast to the generally low correlation between annual catch and the total squid sampled.

Several components were distinguished in this study. Coelho (1986) found that the winter-spawning component was the most abundant and consisted of squid in the size range 180-240 mm in sub-area 3. This would correspond to component 4, the winter-spawners, in this study. A summer-spawning component is also known for this species and may at times be relatively abundant (Squires, 1967; Lange and Sissenwine, 1983; Coelho and O'Dor, 1993), corresponding to component 3 in this study. These two components (3 and 4) were consistently found in all areas. Coelho (1986) describes further a component (component 5) in sub-area 3, characterized by large

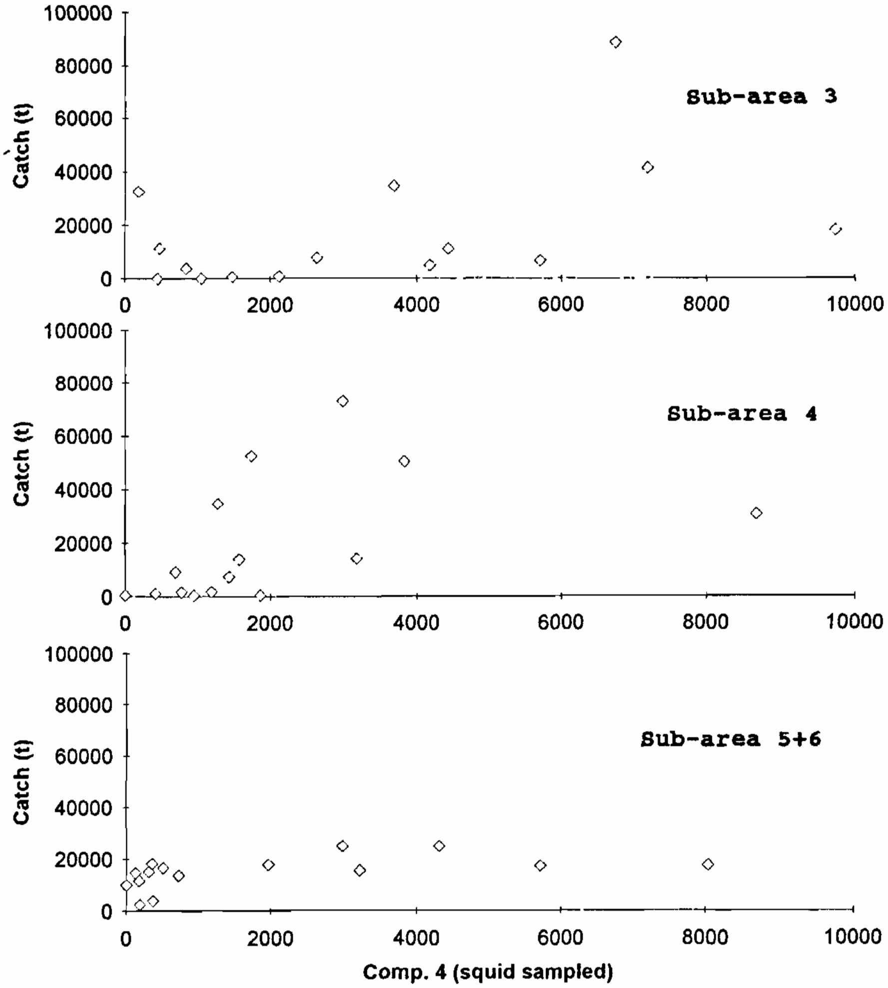

Figure 4. – Relationship between annual catch and number of component 4 squid sampled for a particular year presented by area. Kendall correlation coefficients are: 0.390 (Pr > R: 0.04) for sub-area 3; 0.467 (Pr > R: 0.02) for sub-area 4; 0.486 (Pr > R: 0.01) for sub-area 5 + 6.

immature squid, which indicates that the one-year life cycle could be prolonged. The capacity to prolong the one-year life span has also been suggested by Squires (1967).

In sub-area 5 + 6, it was possible to distinguish further components 1 and 2. It was not possible to determine if components 1 and 2 represent different life cycles or, if their presence was a result of the capacity to shift between life cycles. Components 1 and 5 may be the same component sampled at two stages in their life cycle due to a prolonged life span.

There was clear geographic variability in complexity of population structure and the annual catch. Five components were identified, including two prominent life cycles; summer and winter spawners. Component 5, characterized by large immature squid (Coelho, 1986), represent the capacity to shift between life cycles. The most southern area was characterized by the most complex population structure. Annual catch was related to the number of component 4 squid sampled, the winter spawners, in all areas.

Life history strategies

The relationship between abundance of the winter-spawning component and the annual catch emphasizes the productivity of this component. Since the population structure is least complex in the northern areas, the catch will be more dependent on the productivity of the winter-spawning component. Abundance, especially in the northern areas, is likely regulated by the environment (Dawe and Warren, 1992). Low abundance in the northern areas in some years may be due to direct environmental effects on productivity or on physical transport mechanisms such as the Gulf Stream Frontal Zone (A. Bakun and J. Csirke, pers. comm.). Alternatively, adverse environmental effects may be indirect, resulting (for example) in asynchronous timing of peak spawning in relation to the seasonal production cycle or transport mechanisms.

As the latitudinal range of *Illex illecebrosus* is very broad extending from tropical to temperate waters,

Table 5. – Population characteristics by area and year. Total sample frequency and the number belonging to components 1 to 5 are given. Also, the number of components observed in the population and the catch data are presented.

Area	Year	Nr. of Comp.	Total (freq.)	Comp. 1 (freq.)	Comp. 2 (freq.)	Comp. 3 (freq.)	Comp. 4 (freq.)	Comp. 5 (freq.)	Catch (tons)
3	1965	3	4 342	–	–	1 273	2 634	435	7 831
3	1966	2	11 937	–	–	7 755	4 182	–	5 017
3	1967	2	11 336	–	–	5 634	5 702	–	6 907
3	1969	1	447	–	–	–	447	–	21
3	1970	1	1 050	–	–	–	1 050	–	111
3	1971	2	5 678	–	–	3 551	2 127	–	1 067
3	1973	1	1 481	–	–	–	1 481	–	620
3	1975	2	1 075	–	–	–	844	231	3 764
3	1976	2	971	–	–	–	479	492	11 257
3	1977	2	237	–	–	–	177	60	32 748
3	1978	2	10 025	–	–	2 834	7 191	–	41 369
3	1979	2	8 051	–	–	1 304	6 747	–	88 832
3	1980	3	6 456	–	–	451	3 690	2 315	34 779
3	1981	2	10 476	–	–	–	9 740	736	18 061
3	1982	2	7 835	–	–	3 403	4 432	–	11 164
4	1970	3	750	–	29	311	410	–	1 274
4	1971	2	1 445	–	10	–	1 435	–	7 299
4	1972	1	1 187	–	–	–	1 187	–	1 842
4	1973	2	769	–	–	88	681	–	9 255
4	1974	1	1 865	–	–	–	1 865	–	389
4	1975	2	1 600	–	27	–	1 573	–	13 993
4	1976	1	8 675	–	–	–	8 675	–	30 510
4	1977	1	3 832	–	–	–	3 832	–	50 726
4	1978	2	1 815	–	–	70	1 745	–	52 688
4	1979	2	3 182	–	–	191	2 991	–	73 259
4	1980	1	1 280	–	–	–	1 280	–	34 826
4	1981	1	3 177	–	–	–	3 177	–	14 142
4	1982	2	852	–	87	–	765	–	1 744
4	1983	2	1 438	–	867	571	–	–	421
4	1984	2	1 398	–	462	–	936	–	404
5	1970	4	635	313	51	78	193	–	2 453
5	1971	2	429	–	–	57	372	–	4 036
5	1972	4	670	125	74	346	125	–	14 713
5	1973	2	354	–	–	48	306	–	15178
5	1974	3	585	–	57	18	510	–	16 653
5	1975	2	2 602	–	1 878	–	724	–	13 790
5	1976	1	4 305	–	–	–	4 305	–	24 936
5	1977	3	3 090	–	78	31	2 981	–	24 883
5	1978	4	9 900	90	687	1 089	8 034	–	17 568
5	1979	3	8 895	–	720	–	5 710	2 465	17 341
5	1980	3	3 201	–	89	1 141	1 971	–	17 864
5	1981	3	4 214	–	259	–	3 220	735	15 574
5	1982	3	1 026	–	242	428	356	–	18 188
5	1983	2	253	–	80	–	173	–	11 598
5	1984	2	1 115	41	–	1 074	–	–	9 938

effects which regulate the proportions of winter –and summer– spawning components may be multiple and interacting. The success of the species in any area may depend on constraints of space and time. The main spawning peak in winter is probably limited to temperatures > 12.5°C in the southern part of the Gulf Stream depending on season (O'Dor *et al.*, 1982). Protracted spawning, reflected by the existence of several components, likely results in extension of the spawning area toward the north, for seasonal spawning components other than winter. Korzun *et al.* (1979) note the presence of *Illex illecebrosus* on the Mid-Atlantic Ridge during a period of high abundance. This would likely be a result of spawning in the northern Gulf Stream by a larger than usual off-season (*e.g.* summer) spawning stock. Spawning success of the winter component is expected to be time-constrained so as to coincide with seasonal productivity peaks in northern areas.

Feeding success is space-constrained in that best feeding conditions occur, in some years, at the northern limit of the range of distribution. While in the southern areas competition appears to be important in limiting feeding success, protracted

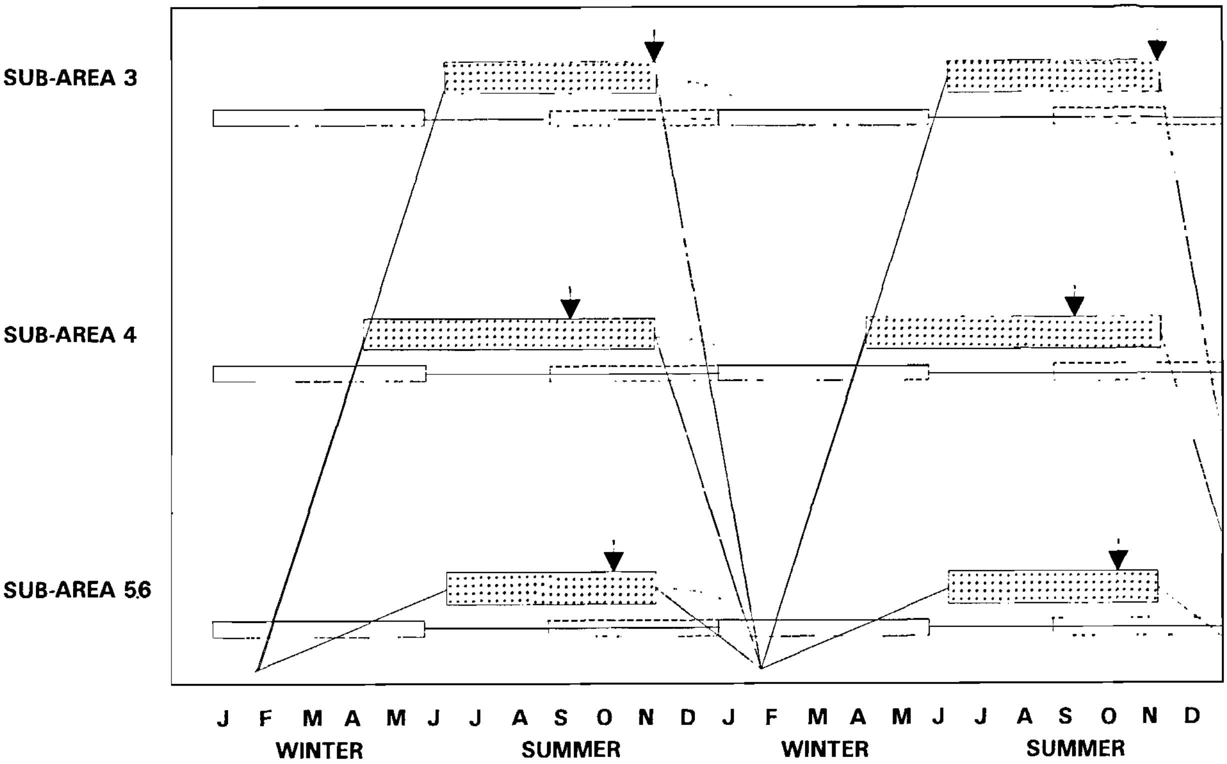

Figure 5. – Schematic illustration of the winter- (large rectangles) and summer-spawning (small rectangles including dashed outline) life cycles. The rectangles indicate time spent in fishery areas, while the solid lines indicate migration and/or spawning away from fishing grounds. Protracted spawning is more pronounced for summer spawners as indicated by the dashed portion of the small rectangles. Solid arrows represent the peaks of occurrence of mature squid indicating the start of migration southwards for the winter spawners (Coelho and O'Dor, 1993). Broken curved lines indicate an interaction between these two components.

spawning promotes stable annual recruitment and thus relatively stable catches. The advantages of good feeding conditions may overcome the risks associated with long-range migrations. We conclude that a northward feeding migration and a southward spawning migration represents the most common strategy of squid of the winter component, whereas other components tend to "stay at home". This non-migratory strategy is one whereby squid that remain at low latitudes compromise feeding success to ensure stable recruitment through maintaining a complex population structure and protracted spawning. This compromise in feeding success would lead to a smaller size, a production of smaller eggs, and a lower fecundity in warmer waters in contrast to squid that spawn in relatively cold waters, as suggested by Laptikhovsky and Nigmatullin (1993).

The two life history strategies discussed, migratory and non-migratory, coexisting most closely in the southern area, are governed by different scales of time and space. The question is whether an interaction exists between the two strategies and if so, how it operates.

Seasonal inshore-offshore movements are normal throughout the distributional range of the species, which can be viewed as a means of enhancing feeding success. Apart from these inshore-offshore movements, the northern winter-spawning squid tends to perform extended migrations between southern and northern areas, being located in the north during summer. An attempt to diagrammatically describe the winter-spawning component 4 is illustrated in *figure* 5. In the same figure, the summer-spawning component 3 is represented. An interaction of the two components would lead to small changes in the one-year life span and in the spawning periods (*e.g.* large immature squid observed in the early winter), also suggested by Squires (1967). It is concluded that the interaction of the two strategies may be frequent at low and intermediate latitudes through the changes mentioned above. At low latitudes, where the two main life history strategies most closely interact, it is expected that cross-generations may be frequent, leading to a complex population structure as substantiated by the data.

Recent results in statolith ageing studies substantiate the idea of more-or-less continous minicohorts, *i.e.* age structure is complex, resulting from protracted spawning (Dawe *et al.*, 1985; Dawe and Beck, 1992; Arkhipkin, 1993). With the validation of the statolith ageing technique, it has become clear that future studies on squid population dynamics should concentrate on maturity and age data (Rodhouse and Hatfield, 1990), since length characteristics may be very variable. This will allow the study of possible interactions between components and variability in life span over several years. It would also be important to consider migration in sampling schemes, as was shown by Arkhipkin (1993) for *Illex argentinus*, since the dominant component of *Illex illecebrosus* is a migratory component in the most northern areas of its distribution.

The fact that five components, characterizing two prominent life cycles, appear mixed throughout the whole distributional range illustrates the complexity of squid populations. A failure of recruitment in the winter-spawning component in northern areas is not catastrophic, because a relatively stable winter-spawning component exists in the most southern area and serves as a reserve. Furthermore, squid of other components may contribute to the winter component through cross-generations.

The interaction between the two life history strategies, migratory and non-migratory, and the two life cycles may partially account for the existence of transition phases between periods of extreme squid abundance (*fig.* 3). Such transitions, particularly in the northern area, may be related to changes in spawning times and duration of generations.

Another interpretation of this data could be that *Illex* have a "circannual" rhythm. This is analogous to a circadian rhythm, *i.e.* an internal clock which has a period of about 24 hours that normaly gets reset by the sun every day. If squid naturally spawn in a little less than a year, it would produce a continuously regressing cycle that would cause varying ages, ensuring continuous production in the tropics. Travelling far north to cold water might slow the clock and produce a stock that "locked on to" an exact one-year cycle that would be self-reinforcing and produce a huge buildup of stocks until they collapsed under competition, or fishing, or climate variability.

A strategy involving a complex population structure may be more generally applicable to broad-ranging ommastrephids in the southern portion of the distribution (northern portion in the southern hemisphere). A life history strategy for squid utilizing disparate feeding and spawning grounds in different seasons is concluded to be stressful. A less stressful, more stable coexistence of the two strategies is restricted to a geographical range that allows compromise between proximity to spawning area and abundance of food, as described for *Illex illecebrosus* in the southern-most fishery area. The overall resultant life history strategy for *Illex illecebrosus* is one that ensures survival of the species by stabilizing recruitment in at least one (southern) area through protracted spawning, complex population structure and interaction of spawning components.

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