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Growth and life cycle of squid,
Loligo pealei and *Illex illecebrosus*

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Introduction.

Samples of squid *Loligo pealei* and *Illex illecebrosus* from the Georges Bank area were analyzed and particular attention was given to their structure with regard to size and sexual maturity. Component size groups were extracted and their evolution was studied.

At this point, the classical growth schemes known for the species were found unsatisfactory since some groups could not be included. Both species however were found to show identical seasonal size distributions and above all maturation process to those of some related European species.

By reference to studies on one of the latter, the same effects are assumed to have similar causes, and new schemes are established in which two growth and reproductive cycles are differentiated. They account for the presence of all the size groups, for their stages of maturation and for the observed spawning seasons.

By the way, an approximate age is given to each observed group.

- Material and methods -

The main sources of information are the data collected aboard R/V CRYOS during the squid surveys carried out in May and September-October 1973, September-October 1974, May and November-December 1975, on Nova-Scotia, Georges Bank and its vicinity. In August 1975, samples were caught by R/V THALASSA off the southern coasts of Newfoundland.

Aboard, immediately after sorting, squid are sexed and Dorsal Mantle length measured to the half-centimeter below, each species and sex apart. Stages of sexual maturation are recorded after a scale proposed by MERCER (1973 and personal communication).

Length frequency distributions are analyzed graphically on probability paper, after a method described by HARDING (1949) and improved by CASSIE (1954) : each component of a polymodal distribution is fitted to a normal curve, and the modal value, identical to the mean in the normal distribution, is determined ; the relative abundance of each size group is also provided. Since each sex is analyzed separately, the percentage given here represent the share of males (or females) in the group to the total number of males (or females) in the catch.

The separation of sexes is quite necessary : first of all because the sexual dimorphism in size, particularly above 10 cm M L, makes the analysis of size data when pooled very inaccurate, also the fact that two analysis are made for the same sample so that we can check whether an extracted group has an equivalent in the other sex.

When subsampling is necessary aboard, an expansion factor is applied so that all the length frequencies are relative to the whole catch in a given area or season.

Growth rates and the evolutions of size groups are estimated from mean lengths ; certainly, it is not a perfect index but, because of significant year-to-year variations, the absolute value has little meaning, and it is better to speak in terms of mean. To my opinion, the important point to take into consideration when an estimate of age is to be given to a group, is the relative position of the successive modes on the histograms together with the modal value itself. Anyway, we may not expect the error on age to be inferior to one month when we study these difficult species from their population dynamics.

The life cycle patterns presented in this paper are drawn so that the age estimates come to the most appropriate interval.

A significant error is committed in the graphical calculation of mean in the groups of little squid most affected by trawl selection ; theoretically, CASSIE's method allows the reconstitution of the real distribution on the whole range, but the skewness observed in frequency curves of squid would anyway make this calculation useless. Let us only assume that the calculated mean is exaggerated to its maximum value.

Basic assumptions.

When problems arose in the comprehension of our observations, informations were sought for in the literature. Obviously, the works by SUMMERS (1968 - 1969 - 1971) and SQUIRES (1957 - 1967) were read in priority ; none of the observations by these authors may be neglected, and if I dare bring some improvement to their conclusions, their studies remain essential. Further help was looked for in the Research Documents presented to this Commission, among which those by MERCER (1973 - 1975) and TIBBETTS (1975) are to be cited.

Populations structures of European species of squid were studied by MANGOLD-WIRZ (1963) in the Mediterranean and HOLME (1974) in the English Channel.

The author's unpublished studies of cephalopods in Bay of Biscay, France, will be referred to in this paper since it was found that Northwest Atlantic species have similar population dynamics to those of Eastern Atlantic, themselves having the same behavior as Mediterranean species. The same structures and evolutions are observed in Loligo pealei and Loligo vulgaris, and to a lesser degree in Illex illecebrosus and Illex coindetii.

Comprehensive studies of the cuttlefish Sepia officinalis have been very helpfull for understanding the life history of Loligo vulgaris and now for that of L. pealei, these three species showing identical physiological reactions to variations in the environment. For this reason, the results of studies on the cuttle-fish will be exposed.

In southern Bay of Biscay and in the Mediterranean, 3 successive "generations" migrate inshore every year : very large animals come to spawn in early spring, then smaller cuttlefish spawn in summer, followed by young immature animals ; the latter feed abundantly and grow fast during their summer period inshore, but in spite of their large size, still are immature when they move offshore in autumn and it was assumed that these individuals would spawn in deep waters during winter time. Each of these successive group could be characterized by a particular shape and structure of the cuttlebone, so that authors had told them distinct species or races.

By a study of the formation and evolution of the cuttlebone, MANGOLD (1966) has clearly demonstrated the interrelations between these forms : the variations in shape and structure of the cuttlebone are related to the phases of growth and sexual maturation, particularly in females, and, in winter, while the cuttlefish is suffering slower growth and is maturing, its cuttlebone is transformed into the form typical of mature animals. So it was demonstrated that the large spring spawners are the same individuals which left the coasts in the beginning of previous winter, and that the forms are linked. The existence of two distinct reproductive cycles was shown thanks to this anatomical piece, and, since a nearly absolute post-breeding mortality is assumed as in other species, the existence of two life cycles.

The physiological background was evinced by RICHARD (1966-1967) when he found that two principal external factors are involved :

With higher temperature, growth and maturation are accelerated.

A long-night photoperiod releases the inhibition to the maturation, in females by central nervous system, males being more independant of this factor, while on the contrary long-day photoperiod or intense light inhibits ovarian maturation but induces egg-laying by mature females. This predominant action of light is the reason why maturation occurs during winter.

By summing both factors, RICHARD came to the following conclusion which, to my opinion, is essential for understanding our observations on squid species studied here. The reproductive, thus life, cycle is fully determined by the time interval separating hatching and the first winter.

Let us consider a squid hatching in spring. High temperature during summer allow a fast growth and it is a fairly developed organism that enters the first winter, so that it may be sensitive to the decrease of day length ; maturation is induced. This, together with the slower growth because of lower temperature, induces the transformation of the cuttlebone in Sepia. Maturation will continue in spring, and the rather small sized cuttlefish or squid will spawn in summer at an age of about 14 months. If now we consider those squid hatching in summer, their organism is not developed enough at the time of first winter and their ovary cannot mature in spite of the favourable light conditions, while on the contrary their growth is heavily affected by lower temperatures. During the following summer, long and intense day light as they are in shallow inshore waters inhibits the maturation, but feeding and growth are intense. Maturation will take place during the second winter, and in spring, large sized squid come inshore to spawn at an age of about 18 months when increasing daylight induces egg-laying.

Starvation was found to release inhibition to the maturation of Illex illecebrosus from Newfoundland (ROWE and MANGOLD, 1975). The squid would then mature in poorer deep-waters after leaving the shelf where it has been actively feeding during summer. Since this factor would have an action in winter only, and on large enough animals, the interpretation given above has not to be changed.

The physiological mechanisms exposed let us understand how, from an extended breeding-season, two reproductive cycles become distinct in temperate environment. Similar phenomena will now be assumed in the explanation of growth and life cycles of Loligo pealei and Illex illecebrosus from the Northwest Atlantic :

In both species, 3 main components are found to migrate successively ; two breeding seasons or peaks are observed with 2 of the components involved, and maturation of females takes place during winter season.

I - Loligo pealei.

The size groups are described, then their evolution is discussed.

A. Analysis of size distributions.

In September and October 1973, trawling stations were occupied on Northern Georges Bank and the following size groups were found :

- (1) 36 p.cent of the males and 44 p.cent of the females had Mantle Length ranging 5 to 10-12 cm, the calculated modal lengths being 9.6 and 9.7 cm respectively, probably exaggerated as was said. They were particularly present on strata 14 and 19.
- (2) The main component of the population consists in males 10 - 12.5 - 12 cm (53 p.cent) and females 10 - 12.2 - 16 cm (45 p.cent), distributed on the whole area. We must notice however an important shift of the mean sizes in stratum 19 where they come to about 15 cm, indicating that larger animals tend to have a more extensive distribution to the North.
- (3) The last 11 p.cent include the largest animals of the population with, as usually observed, a mixture of age groups. A modal length was calculated at 17.1 cm for females, males showing a correspondant mode on the 19 cm class, while larger males have mantle lengths 22 - 31 cm. This group also is better represented in strata 13 and 19.

A more extended area was surveyed one year later in September and October 1974, and the observations on squid were described by PAULMIER and MESNIL (1975), but corrections are to be made. First, young specimens had not been sexed and could not be included in the distributions, now, on the basis of the usually observed 1 : 1 sex ratio in these young, 50 p.cent have been added to the length data of each sex. Besides this, the particular groups sampled in the South had been analyzed quite apart, so that their relative position and importance could not be appreciated ; now they are pooled with other samples. The following distinction of groups is preferred :

- (4) Some 30 p.cent of the catch are young squid 2 - 10 cm in Mantle Length, with a mean size at about 6.5 cm, distributed only to the North of 39°30 N, and relatively more abundant in deeper waters. A decrease of their modal size from shallow to deep waters was also noticeable.

- (5) The most important component (about 60 p.cent) is the group formed with males 9 - 14.6 - 21 cm and females 9 - 13.5 - 18 cm. These ranges and modal sizes show very important geographical variations, as they significantly decrease to stratum 6 and to the South of Hudson Canyon. Most members of this group still are immature.

- (6) Squid larger than 18-20 cm are irregularly distributed on the area. Here again, males 19 - 23.2 - 30 cm and corresponding females 16 - 18.4 - 24 cm are probably mixed with males 30 - 35 cm present in little number. Most males are mature, and females near maturing.

The same area was surveyed in May 1975 and 3 groups were found :

(7) 44 p.cent of the males and 57 p.cent of the females are squid 5 - 10 - 12 cm, nearly all immature, females particularly. They are mostly abundant on the edge of the shelf to the South of Georges Bank, between 60 and 100 fms.

(8) Males 10 - 15.4 - 18 cm and females 10 - 13.2 - 17 cm form the second strong class in the population ; their relative importance is 44 p.cent and 42 p.cent respectively, certainly more if we think that most members of the group may have already reached the coastal zone. Males and females are mature or late maturing and most females, even immature, are fertilized.

(9) Squid larger than 20 cm are predominantly males, with maximum size at 33 cm, females reaching 24 cm. It is assumed that the bulk of squid belonging to this group either has migrated inshore, or has already spawned and died in inshore or deep waters. They are mature animals, and large egg-clusters have been found in 100 m deep waters of stratum 11.

The last sample analyzed was collected on Georges Bank and South of Nantucket Shoals between November 27 and December 11, and then again 3 groups were identified :

(10) Squid with Mantle Length 4-14 cm are widely predominant in this season (80 p.cent) and present in the whole outer shelf where stations were occupied. Modal sizes at 11.3 and 10.9 cm are determined for males and females respectively.

(11) Squid forming the second size group covering the classes 11 to 17-20 cm are very hard to separate from group (10), except on strata 3 and 4 and on the slope to the South of Georges Bank. This tendency would indicate that a majority has left the shelf towards deeper waters or to the South, the remainders being smaller squid of the group. Males have mean lengths 14.6 to 15.5 cm females about 13.5 cm, and their relative abundance are 11 p.cent and 27 p.cent respectively, but all these figures probably are underestimates.

(12) The tail of the distribution is formed with a little quantity (3 p.cent) of large squid of which tentative mean lengths are 22.5 cm and 19.3 cm for males and females.

In all seasons, the populations are formed with two main components, the third one being a mixture of scarce individuals probably belonging to 2 age groups at least.

B. Growth and age.

Year-to-year variations are important as observed between groups (1) and (4) or inside group (2) or (5), but from the relative positions of the modes, it is possible to identify equivalent groups in samples from different years.

Squid sampled in Northern areas use to have larger size and we may consider that group (1) is formed with large individuals of a group characterized in 1974 as (4) and met as (10), then 2 months older, in 1975.

Groups (2) and (5) have similar mean lengths at the same season and show similar North to South variations that indicate an active offshore migration, also affecting the equivalent group (11). Same equivalences are found in corresponding groups of large squid.

When fall and spring components are compared, the most probable origin of group (8) is group (10) from November-December, or groups (1) or (4) from September-October samples ; since the mean length of squid in (7) is only 10 cm, they may not be issued from (10) but belong to a separate progeny. In the same way, groups (2) and (5) are composed of grown-up from group (7). The first steps of our growth schemes is :

(1) or (4) → (10) → (8) and parallely, (7) → (2) or (5) → (11).

For solving the problem of age, the presence of mature squid and egg-clusters must be taken into consideration. In the first weeks of May 1975, fully mature squid of both sexes and eggs were found offshore and the bulk of breeders is supposed to have already migrated inshore and spawned. So, near the Northern range of the species, the first breeding period is April-May, and I assume that it is earlier in the South ; hatching may begin in June that we consider as origin of time.

Young-of-the-year appear for the first time in fall as groups (1) and (4), then 5 months old, and their mean length is 8 cm approximately (7 to 9 cm). Between June and September-October, during summer months, their monthly growth rate has been 1.7 to 2.0 cm.

In late fall, group (10) is met with a mean length at 10-11 cm, at an age of 6 months : it grew 1.6 to 1.8 cm a month since hatching, but only 1 to 1.5 cm a month since September. These rates are identical to those calculated by SUMMERS.

When (8) is found in May, then nearly 1 year old, males are 15 cm and females 13 cm, and both sexes are maturing or mature. During the 5 winter months their monthly size increment has fallen to 0.4 to 0.6 cm, thus an average of 1 cm a month when calculated from September-October ; the noticeably slower growth during winter leads to an average growth rate of 1.2 to 1.3 cm a month between hatching and 11 months of age.

If we consider the parallel sequence from (7) to (11), a monthly increment of about 1.2 cm between September-October and May as found above is taken as a basis.

With a mean length at 9-10 cm, squid belonging to group (7) must be about 8 months old, thus spawned and hatched during the previous summer, about August-September. Their ulterior growth till fall is only 1 cm a month, and this shows that they still are strongly affected by the low temperatures during their first winter. Their maturation takes place during the second winter and they ~~come~~ come back to spawn in early spring then 20 months old and their size is about 20 cm.

If now we think of their "parents" spawning in August, the only mature squid at that time are those belonging to group (8) in May : their age at breedings is 14 months. The two cycles are illustrated on fig. 3.

By that way, two reproductive cycles are determined : squid hatching in spring spawn during the following summer at an age of 14 months ; their progeny remains immature during the following year and comes to spawn in the next spring at an age of 20 months. Thus ~~it~~ it is shown that the two cycles are crossed, a phenomenon already observed in European Sepia officinalis and Loligo vulgaris.

Only the two main components of each sample were considered here, but the larger squid are also involved and many of them, males particularly, can breed a second time and be mixed with squid from younger groups on the breeding areas. In some cases, large squid may have remained immature during two years.

C. Discussion.

In the schemes proposed, two main modifications are brought :

- the existence of two life cycles that are not fully separated but crossed ;
- November brood is replaced by an earlier summer brood.

The latter was preferred to SUMMERS's hypothesis primarily because this author gives no mention of mature squid in November, only supposing that they remain to the South, and the latest records of spawns are in September, fitting better to our scheme.

In this paper, ages are estimated from the average growth rate of squid of the other "generation" at the same period, and breeding is found to occur at a season when mature spawners are actually present and records of spawn in the literature are consistent.

A particularity of the size distributions observed in spring and fall, at nearly half-year interval, must be noticed since it is a first clue of the existence of two generations a year and, to a lesser degree, of crossed cycles. In May and in fall, the two first components have similar mean lengths : 10-11 cm in (7) and (10) ; 13-15 cm in (2), (5) or (11) and (8), and large squid 20-30 cm are also present in both seasons. A natural conclusion is that the first component in May has grown to the second fall component ; (10) to (8), and on the contrary (2) or (5) are issued from (7). The real link between these groups is finally demonstrated by the analysis of samples and the study of their growth and maturity, as was done here.

When the determinism of the two cycles was explained for Sepia and inferred for this species we started from fully separated hatching periods to give a clearer idea of the mechanism, and size was used to estimate the ability of maturation. In fact, we can observe that breeding seasons are long with sometimes peaks in spring and summer, and this is due to the fact that the period of maturation itself is long. Since the actual determinism is physiological, it is rather independent of the exact age of the squid, and some individuals from the summer brood may mature while some from the spring brood do not. All depends on the condition of the animals and on its sensitivity to the variations of environmental factors. On the other hand, only the induction of maturation may happen during winter, but full maturity may be reached much later. By the way, an extension of the maturation period leads to an extension of the breeding periods.

During the following year, breeders born at both seasons may be mixed in the spawning areas.

Actually, if the reproductive cycles were fully determined by the date of hatching, an impossibility would arise. If we start from a year with both spring and summer hatching, we should find only summer spawners during the following year, then only spring spawners during the second year and the original situation should be met during the third year. A supplementary 3 year cycle would appear, and as far as we know it has not been noticed.

Both geographical variations in size and structure and migrations of the species show a significant North-South axis, and Loligo pealei is assumed to be a primarily meridional species.

When we consider the Georges Bank area, near the northern limit of the species, this affinity may cause delay of the date of arrival of large spring spawners, and probably the smaller summer spawners are poorly represented. In that particular meaning, I agree with SUMMERS's assumption of the second yearly brood to occur in the South, but we have shown that late born squid have on the contrary a very wide distribution when they are older.

The same variations of the characteristics and behavior of populations are observed in European waters. In Bay of Biscay, Loligo vulgaris migrate on very short distances between coasts and deeper waters ; large spring spawners come inshore very early, and offshore migrations begin very late ; two reproductive cycles are observed, and summer breeders are well represented.

In North Sea, only large squid migrate and spawn, in May, and individuals from other groups are very scarce. The migrations proceed on long distances and along a principal North-South axis. To my opinion, the observations by TINBERGEN and VERWEY (1945) may only concern the seas near the northern range of the species, while the biology of the species in Southeastern Atlantic shows the same pattern than in the Mediterranean. HOLME (1974) has also observed that Loligo vulgaris from the English Channel spend the winter months off the western entrance of this sea, and not off the portuguese coasts, and my observations are consistent with his.

Another behavior is found in Northwest African waters where the species stays inshore all the year long.

II - Illex illecebrosus.

As was done with Loligo, size groups are described and their growth and cycle discussed.

A. Analysis of size distributions.

(1) In May 1973, short-finned squid were caught on Northeastern tip of Georges Bank, Nova-Scotia and Grand Banks ; their size range and mean are 9 - 14.1 - 18 cm for males, 10 - 14.3 - 18 cm for females, with mean lengths significantly higher on Nova-Scotia and Georges Bank (MERCER and PAULMIER, 1974). Five males 14-16 cm from the Southern part of the surveyed area were found to be at stage I, others being immature.

A mature female 30.5 cm, mated, was caught, and two females 21 cm had slightly enlarged nidamental glands.

In September-October 1973, 3 groups were found on Northern Georges Bank :

- (2) A very little number of young squid (1 p.cent of the total number) was met with size range 7-15 cm ; most were found in shallower strata.
- (3) 44 p.cent of the males and 41 p.cent of the females have size range and mean 15 - 18.5 - 20 cm and 15 - 19.0 - 21 cm respectively. They tended to be more abundant on shallower strata 19 to 21.
- (4) 55 p.cent of the males and 58 p.cent of the females have size distributions 18 - 21.1 - 24 cm and 19 - 22.0 - 26 cm, and were mainly found in deep waters of the southern slope of Georges Bank, probably leaving the shelf.

Maturity stages of these squid were not recorded.

An identical structure was observed in September-October, with similar mean lengths:

- (5) 3 p.cent of the catch are scattered young squid 6 - 11 cm with approximate (not significant) mean length at 8 cm. They were absent from deep waters and from the South.
- (6) 12 p.cent of the population consist of males 15 - 17.7 - 20 cm and females 16 - 18.2 - 21 cm, only present on strata 2, 4 and 6 to the South of Cape Cod. Most males longer than 18 cm are maturing but all females are immature.
- (7) The main part (85 p.cent) of the population is composed of males 19 - 21.5 - 26 cm and females 19 - 22.9 - 30 cm, only present on the northern part of the surveyed area. Most males larger than 21 cm are mature or late maturing.

In May 1975, only one component was found on Georges Bank and Nova Scotia :

- (8) with males 6 - 15.1 - 22 cm and females 7 - 15.7 - 23 cm, although a few maturing females 25-30 cm were caught. Geographical variations are noticeable since mean lengths of males are 14.3 cm on Nova Scotia (quite comparable to (1)), 15.4 cm on Georges Bank and 15.6 cm to the South of 40°30 N, with corresponding mean lengths of females at 14.6 cm, 15.8 cm and 16.4 cm, thus higher in the South.

Females are immature but a few males larger than 13 cm are at stage I, a few 15-18 cm at stage II and some 14-22 cm mature.

A sample was caught by R/V THALASSA off the Southern coast of Newfoundland on July 29, 1975 :

(9) Size distributions are 14 - 18.7 - 22 cm in males, 15 - 19.4 - 24 cm in females, each sex showing a slightly bimodal frequency distribution with very close modes. A few males 18-21 cm are at stage I but none at stage II. In summer 1975, Illex were very abundant in Newfoundland waters.

Three other groups were found in November-December 1975 on outer shelves :

(10) 60 p.cent of the catch are juvenile males 6 - 11.5 - 14 cm and females 7 - 12.0 - 15 cm, mainly present in the Northern part of the surveyed area, strata 17-18, and on Nova Scotian shelf where they are smaller. Escapement of little squid from the trawl was visible so that the mean size in this group is probably exaggerated.

(11) 32 p.cent are males 13 - 15.5 - 21 cm and females 14 - 17.2 - 23 cm, caught on Nova Scotia and southern slope of Georges Bank, particularly between 60 and 100 fms, but tending to be less abundant to the South. All females are immature while most males larger than 15 cm are at stage I, most larger than 18 cm at stage II and many 18-21 cm are mature.

(12) The last 8 p.cent are formed with the large squid usually caught in autumn. They were found mainly in deep waters, to the South or near Hudson and Corsair Canyons, and this tendency indicates that most have left towards deep waters.

Males sampled have mantle length 21 - 23.7 - 25 cm, females 22 - 25.9 - 30 cm ; all males are mature.

It is interesting to notice the similarity of maturation in groups (11) and (12). If we consider either the relative number of mature individuals to immature or maturing at each size, or the length frequency distribution of mature animals, there are two distinct modes, one in each group.

In this species, the identification of related groups at given seasons is easy : groups (1) and (8) in May are equivalent ; as are (2) and (5) and part of (10) ; (3) or (6) and (11) ; (4) or (7) and (12).

If we refer to SQUIRES's scheme, the evolution of some of the groups is as follows : (1) or (8) → (9) → (4) or (7) → (12).

We still have to understand the origin of the other groups.

B. Growth.

To my opinion, no doubt is permitted about the evolution of mean lengths as observed by SQUIRES and other authors, and ~~is~~ confirmed here to occur on a larger area. A modified growth scheme should anyway include this evolution. From it, an average growth rate is calculated.

Between May and the end of July squid grow an average of 1.8 cm a month from (8) to (9), then 1.2 and 1.6 cm a month from late July to November-December, thus 1.4 cm for males and 1.7 cm for females from May to December.

Higher values are calculated between May and September-October 1973 from (1) to (7) or equivalent group (4) : 1.8 cm a month for males, 2 cm for females. We have noticed however that group (1) from Nova Scotia is affected by regional variation as shown when (8) was described, and that mean size of squid in group (12) might be underestimated because larger squid have left. Monthly increments calculated by SQUIRES are 2-3 cm in males, 1-4 cm in females.

From our data, the average growth rates of males and females are 1.5 and 1.9 cm a month, calculated during summer months when growth is supposed to be very fast. They are used to estimate ages.

With a mean length at 14-16 cm in May, squid in groups (1) or (8) must be 8 to 9 months old, thus hatched in June or July of the previous year.

If now we consider the little December squid in group (10) and suppose that their mean length is slightly exaggerated, an actual mean at about 10 cm leads to an estimated age of 6 months and they would have hatched in early summer of the same year. So these groups are quite probably linked and the large squid caught in summer are issued from the group of little squid very abundant in late fall, hatched in summer.

The sequence would then be :

July brood $\rightarrow$ (10) $\rightarrow$ following year $\rightarrow$ (1) or (8) $\rightarrow$ (9)
 $\rightarrow$ (4) or (7) $\rightarrow$ (12).

When they come to Newfoundland in May, squid in (1) or (8) are not 4 months but 10 months old ; they leave in November and are supposed to spawn in late winter, then about 18 months old.

In groups (3) or (6) from September-October, males have mean length 16-18 cm and females 17-19 cm. If 1.6 cm and 1.9 cm monthly increments during summer are kept, their age is 9-10 months and they hatched in January-February of the same year, thus from squid and the previous cycle. They were found in December with slightly lower means, probably because some have migrated, but their age and origin are not to be changed. We have noticed that many males in (11) were maturing or mature at ~~much~~ much shorter mantle size than squid in (12), and I suppose that they will breed in the first part of the following year. Since group (10) is estimated to hatch in early summer we may think that it is spawned by grown-up of these autumn groups (3), (6) or (11), breeding at an age of about 18 months ; their mantle length at that age is about 25-30 cm.

The second sequence is :

Winter brood by (12) $\rightarrow$ (3) or (6) $\rightarrow$ (11) $\rightarrow$ July brood
in the following year.

For this species also, crossed generations are found to fit the evolution of observed size groups. Two life cycles are determined, with nearly identical durations.

C. Discussion.

As was done with *Loligo*, the first steps to the proposed schemes are :

- Estimation of ages from observed growth rates
- Evolution of sizes and maturities in the observed groups.

The growth rates are calculated in the well known part of the cycle, already described by SQUIRES and most often cited, but different values are found. The differences may be due to the fact that SQUIRES's ages are estimated from an extrapolation of observed data to a mathematical model of which I don't think it is adequate. Life cycles of squid are demonstrated to be short and growth rates show important seasonal variations, moreover when compared to the total duration of the cycle ; so that growth curves have a pronounced stairs-profile. I also remark that both sexes are mixed and cause an overestimate of the mean rate, and the zero-time is forgotten in the exponential. On the contrary, monthly increments calculated from his observed lengths are quite comparable to ours.

It was said that seasonal variations are important, so that our rates calculated for summer period are assumed to be high, if not nearly maxima, values. When Illex come to feed on the shelves in summer, they find together abundant food and optimal conditions for digestion and growth. Even so, the deduced ages are quite superior to those calculated from the model, and lead to longer cycles.

Actually the need for a modified scheme came from the observation of particular size-groups nearly unknown in Newfoundland since only a few elements that we can recognize as members of groups (3), (5) or (11) come there in some years. To the South, these groups are better represented and we may not consider them only as late born or slow grown, moreover when their maturity pattern is analyzed.

The basic link was provided by the important group of young squid (10), already observed during U.S. Groundfish Surveys as shown in figure 8 b of a Research Document by TIBBETTS (1975). When it comes into the shelf in late winter or early spring, this group is widely dominant, and the groups formed with grown-up should be met in equivalent importance in other seasons. So is supported the relationship between these little squid and the large ones also dominant in late spring and summer on Georges Bank or in Newfoundland. We notice also that the modal length of the little squid is under 10 cm in the figure cited above, and the mean length of our group (10) is confirmed to be overestimated.

Besides, maturing or mature males were found in May, and if their age was only 3-4 months, their maturation would be incredibly fast. In the proposed cycles, squid maturing in winter are 1 year or 16 months old.

The duration of life cycle of Illex still is rather approximate. The species is only catchable during the feeding period when females still are immature, and eggs are spawned in deep waters and cannot be found. Eventne larvae are of little help since all squid of the Ommastrephidae have similar Rhynchoteuthis. Thus, breeding period can only be estimated from maturities of males, date of migrations and appearance of young squid.

The same problem is met with Illex coindetii from Bay of Biscay, although a better estimate is provided since maturation begins at smaller size in both sexes, and mature squid and mated females are found in November and in June before their offshore migration. Large winter spawners are caught by trawlers off Spanish coasts and the first breeding period is then known to be in January-February. An equivalent delay between migration and breeding is inferred for summer migrants. In this species also, squid appear on the shelves once or twice in their life, at different stages of their evolution. Usually, they are found together with the related species Todaropsis eblanæ which has similar, but more easy to follow, life history.

A primary meridional affinity was found in Loligo pealei, and the same is assumed for Illex illecebrosus although the latter is more tolerant to environmental variations. Newfoundland Banks are situated near the northern limit of the species, and only one group, formed with large squid, migrates that North; the presence of smaller maturing squid is accidental.

The smallest squid as found in fall don't appear to the North of Nova Scotia in their first year. North to South variations of the mean lengths were also noticed.

The variations in strength of one of the generations, together with hydrological causes, might explain the variations in abundance of summer squid off Newfoundland.

Conclusion.

As a conclusion, some general aspects of the biology of squids are underlined.

Twin crossed reproductive cycles were found to fit the observed evolutions of size groups in both species and, as for the cuttlefish, are assumed to be determined by a physiological response to external factors. Due to their existence, a problem still remains with the possibility of a supplementary cycle.

The breeding seasons and size ranges in *Loligo* are rather extended, so that squid born each year are more or less equally parted towards one cycle or the other, and we can see that breeders are abundant at both seasons.

Things are less easy to appreciate in *Illex* since size ranges are very close to the modes and the groups seem well separated ; besides, summer spawners are difficult to assess since they are scarcely represented at the periods when our samples were caught.

Further studies should cope with the evaluation of abundance of each generation all along its life. The continuity of strength of each group should be controlled so that we can prove the existence of linked, crossed, cycles either with breeders issued from both generations, or from only one and then probably a 3 year cycle could appear.

Some biological characteristics were also found to support particular structures. In short-lived animals as squid, the existence of groups with equivalent mantle length at half-year intervals is a clue to the existence of two generations a year and that two at least of these groups are directly linked.

Seasonal variations in growth rates have been observed in these species and in other Atlantic cephalopods as well, but it is also important to notice that growth of late born squid is much slower all along their life because they are strongly affected by low temperature in winter ; this slower growth also noticeable in European species allows in a certain way to identify squid from late brood when compared with those from spring brood.

Migrations and, to a larger scale, zoogeographical affinities, account for variations in structure, mean lengths or behavior. Larger squid have wider range ; near the limit range of the species, a North-South axis of migration dominates the shore-slope axis, and only one of the components is present for spawning, usually later than in the primary areas, thus causing larger fluctuations in abundance. Each age group has its own migration pattern.

These peculiarities are to be recognized when the actual characteristics of the different groups must be estimated.

The biological informations presented in this paper, above all when such basic parameters as age and growth are concerned, are expected to lead to better precision and significance in quantitative assessments.

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Nota : the author would appreciate entering discussion with persons holding contradictory data.

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LOLIGO PEALEI

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3. IX - 10. X. 1973

4. IX - 14. X. 1974

3 - 19. V. 1975

22. XI - 15. XII. 1975

Fig. 1. Loligo pealei - Size frequency distributions.

Loligo pealei

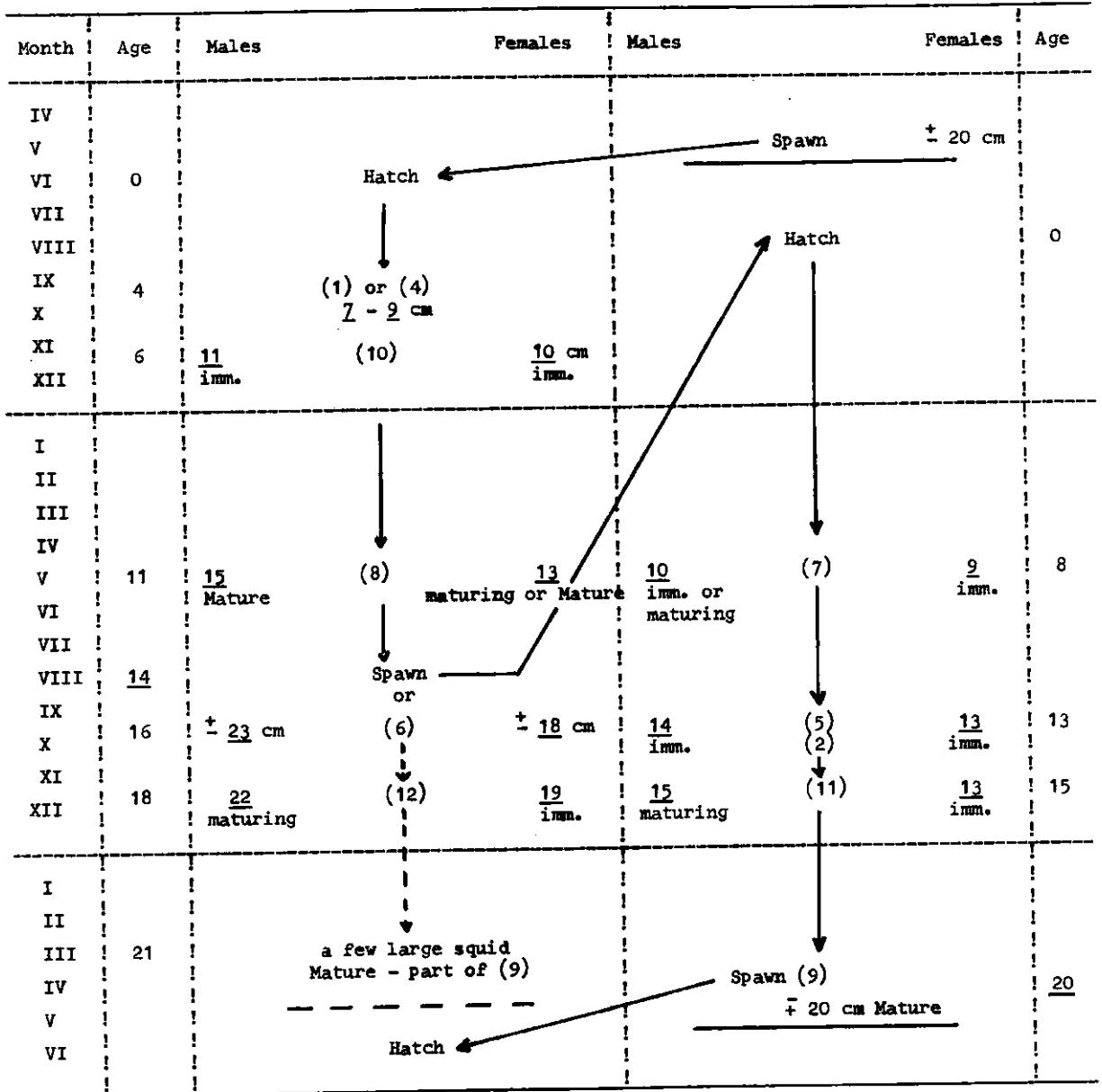


Fig. 3 - *Loligo pealei* - Growth schemes and reproductive cycles.

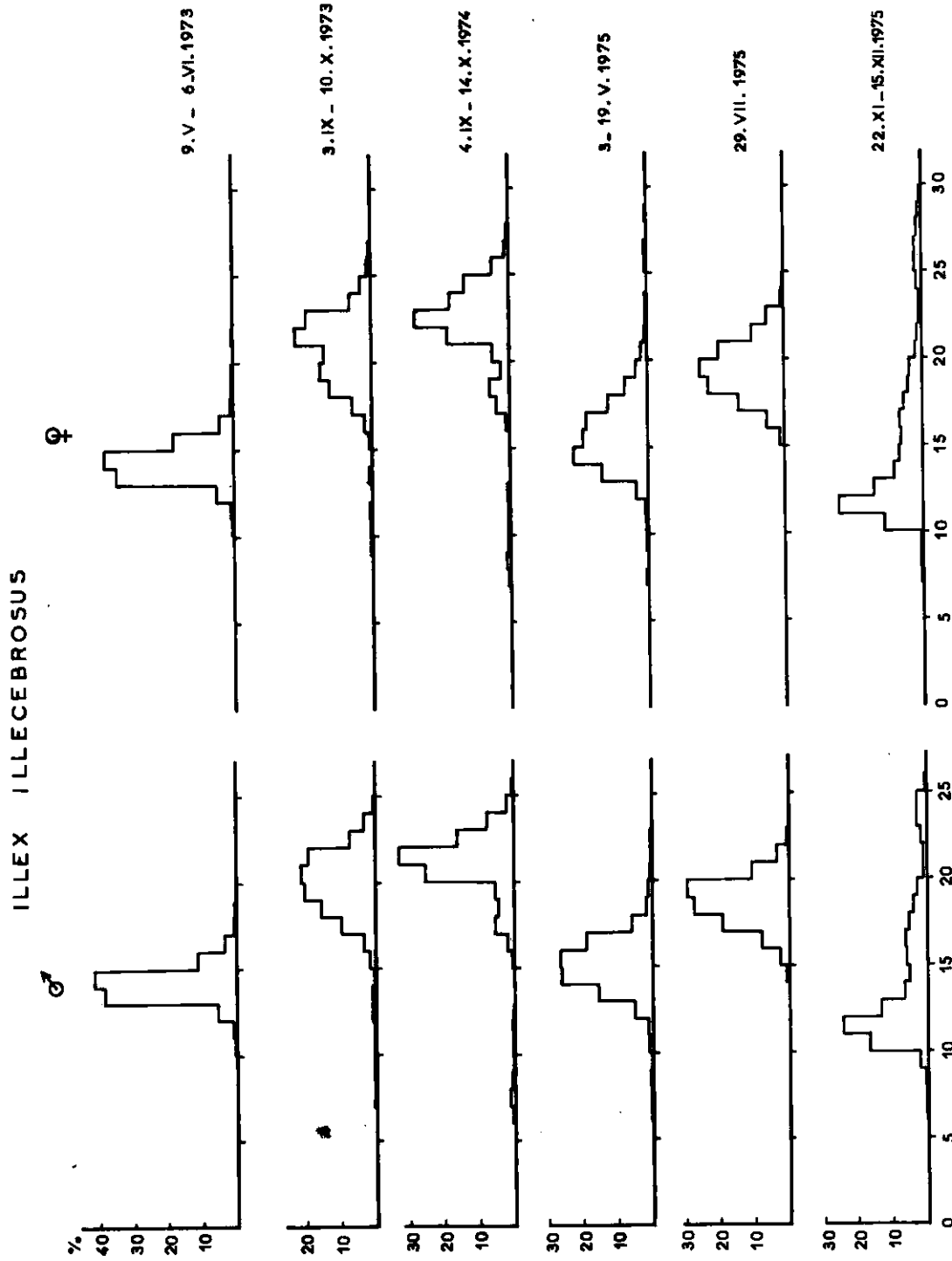


Fig. 4 - Illex illecebrosus - Size frequency distributions.

May 73	M	:	:	:	9 - $\frac{14.1}{(1)}$ - 18	:
	F	:	:	:	10 - $\frac{14.3}{(1)}$ - 18	:
May 75	M	:	:	:	6 - $\frac{15.1}{(8)}$ - 22	:
	F	:	:	:	7 - $\frac{15.7}{(8)}$ - 23	:
July 75	M	:	:	:	14 - $\frac{18.7}{(9)}$ - 22	:
	F	:	:	:	15 - $\frac{19.4}{(9)}$ - 24	:
Sept.Oct.73	M	:	:	:	15 - $\frac{18.5}{(3)}$ - 20; 44%	:
	F	:	:	:	18 - $\frac{21.1}{(4)}$ - 24; 55%	:
Sept.Oct.74	M	:	:	:	15 - $\frac{17.7}{(6)}$ - 20 ; 11%	:
	F	:	:	:	19 - $\frac{21.5}{(7)}$ - 26 ; 86%	:
Nov.Déc.75	M	:	:	:	6 - $\frac{11.5}{(10)}$ - 14 ; 60%	:
	F	:	:	:	13 - $\frac{16.5}{(11)}$ - 21 ; 32%	:
		:	:	:	21 - $\frac{23.7}{(12)}$ - 25 ; 8%	:

Fig. 5 - Analysis of size distributions - *Illex illecebrosus*.

Illex illecebrosus

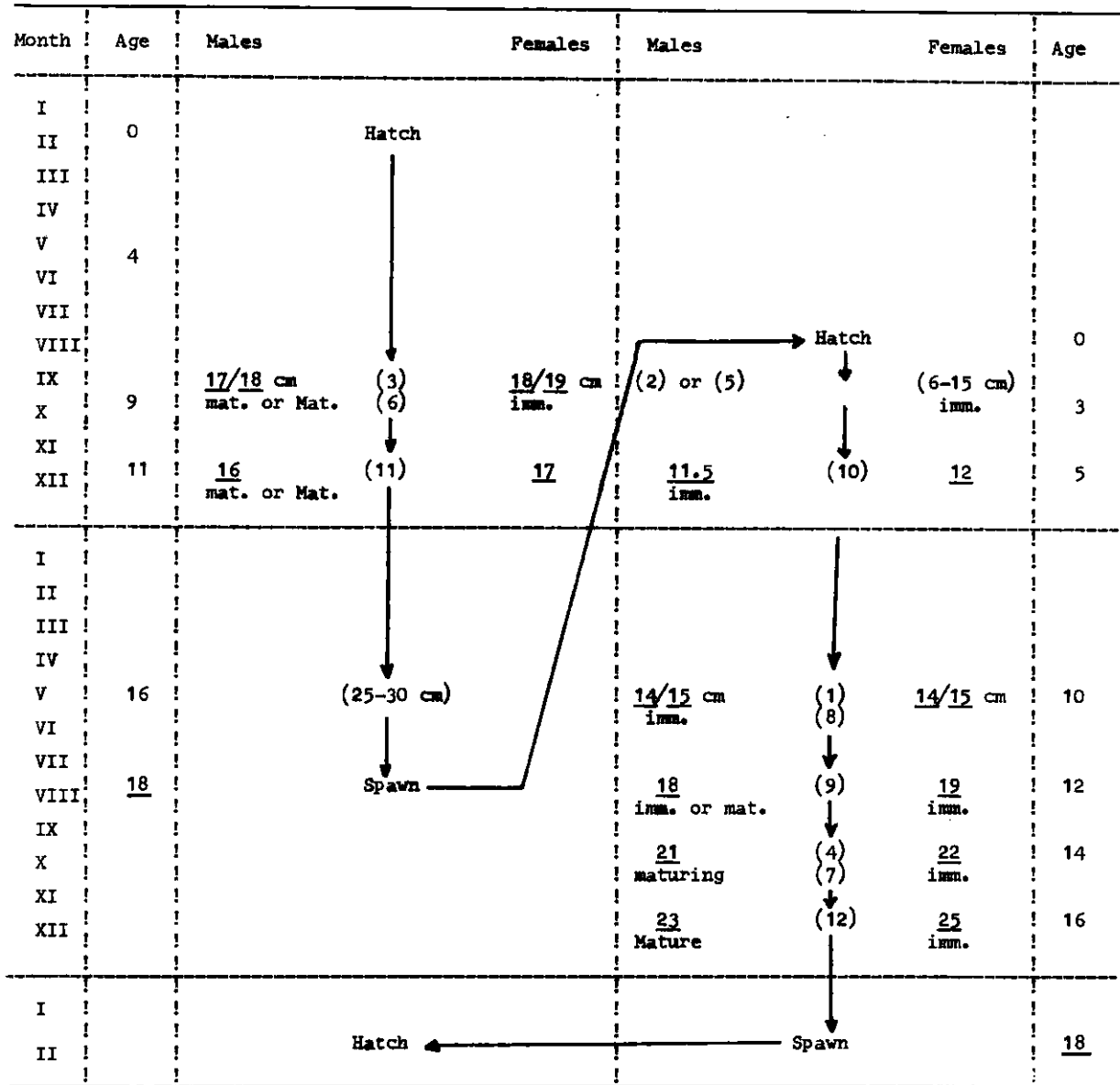


Fig. 6 - *Illex illecebrosus* - Growth schemes and reproductive cycles.