Northwest Atlantic Fisheries Organization

Serial No. N913

NAFO SCR Doc. 84/IX/116
(Summary only)

SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1984

Life Cycle and Mechanism of Abundance Fluctuations in *Illex illecebrosus*

by

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Summary

The life cycle of the short fin squids of the Northwest Atlantic, ranging in the area from the Florida Peninsula to Labrador as a single population (Romero and Amaratunga, 1981; Froerman, 1983; Froerman, Dubinina, 1984), was studied. The data on the distribution and biological parameters of the population in different ontogenetic stages was collected during the 1966 to 1983 period. Information on the distribution and biology of the short fin squids inhabiting the areas south of Cape Hatteras and north of Banquerreau Bank was mainly adopted from the literary sources.

Results of seasonal and year-to-year analysis of the distribution and biological parameters of the population in various parts of the area are in agreement with the communication of Lange (1981) which says that the spawning of the short fin squids occurs throughout the year with a peak in a fall-winter-spring period. Primarily, the spawning takes place in the continental slope pelagial between the Florida Peninsula and 40°N, which is substantiated by the larva distribution pattern (Roper and Lu, 1978; Dawe and Beck, 1982; Hatanaka et al., 1982; Trites, 1982; Dubinina, Froerman,1983; Froerman, 1983; Froerman,Dubinina,1984).

Some squids stay in the spawning area for feeding. The other part of the spawning products represented as egg masses, larvae or juveniles is transported in the northern Gulf Stream edge to the north-eastern region of the species distribution area. From the Gulf Stream juveniles migrate to Georges Bank,

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Nova Scotia and Great Newfoundland Bank (GNB), where they feed and grow. At the end of the ontogenesis the modal mantle length of the squid females, who feed in different parts of the distribution area, increases from 200-240 mm in the south (Mid-Atlantic Bight area) to 250-280 mm in the GNB area (Squires, 1957; Mercer, 1975; Collins and Ennis, 1978; Beck et al., 1980-83; Amaratunga, 1980; Lange, 1981; our data). The maximum potential fecundity of the females increases in the same direction (Durward et al., 1979; Burukovsky et al., in press). Year-to-year fluctuations of abundance in the Mid-Atlantic Bight area are insignificant (Lange and Sissenwine 1980, 1983; ICNAF, NAFO SCS Doc., 1978-1984) increasing in feeding grounds of the area from Georges Bank to GNB (Squires, 1957; Hurley, 1980; Dawe and Hurley, 1981; Amaratunga and Roberge, 1981; IKNAF, NAFO SCS Doc., 1978-84).

The ontogenesis lasts 12 ± 1-3 months (Squires, 1957; 1967; Amaratunga, 1967; our data). The life cycle involves five ecologically isolated stages:

1. Planktonic development stage (embryogenesis, larva, juvenile, ML to 25-30mm). This phase passes in the pelagial of the continental slope waters or in the northern Gulf Stream edge. The duration of the planktonic stage is 20-30 days (Froerman, Dubinina, 1984). The distribution of egg masses, larvae and juveniles during this period depends on the peculiarities of the water mass dynamics in the biotope.

2. Nektonic pelagic development stage outside the shelf. The duration is 2,5 - 3,5 months. During this period the juveniles of 25-30 to 100-130 mm ML feed in the pelagial of the continental slope water and perform an active migration towards the shelf on completion of the pelagic stage. The mean migration velocity is 2.5 miles per day.

3. Nektonic stage of feeding and maturation above the shelf. The duration of this stage in the reproductive part of the area is 7-10 months, and in the feeding ground - 4-8 months. ML fluctuates from 100-330 to 220-300 mm. Rates of growth and

maturation change depending on season and feeding ground.

4. Stage of migration for spawning and complete maturation. The duration is 1 to 4 months. ML of the females is 190 to 130 mm, and of the males 160 to 250 mm. The mean migration velocity is 11.1 miles per day.

5. Spawning. Occurs throughout the year, the major period lasting from September to May. The spawning ground is located between the Florida Peninsula and 40°N in the pelagial of the continental slope.

In the continental slope area south of 40°N the reproductive and feeding parts of the distribution area coincide. This is the "core" of the species range. The shelf waters from Georges Bank to GNB are a feeding or adaptive ground. The squids migrate to this ground from the oceanic and shelf waters, where the egg masses, larvae and juveniles transported by the Gulf Stream accumulate (planktonic stage of the ontogenesis). The area, where the stages of planktonic development and nektonic pelagic feeding proceed can be identified as preadaptive region.The amount of spawning products transported to the adaptive region depends on the Gulf Stream strength and its orientation relative to the mean long term position. For the period from 1960 to 1982 the mean temperature of the slope waters (16°C) in the area between 66° and 50°W was taken as the index of the mean long term position of the Gulf Stream. The more the surface water temperature in that area exceeds 16°C the greater the Gulf Stream strength and the closer its northern edge to the spawning area; as a result, the distance covered by the larvae and juveniles in the north-east direction is greater and the amount of the latter larger. Having attained the 25-30 mm length, juvenile squids migrate from the northern Gulf Stream edge towards the shelf. During the January to June period length classes of juveniles in the area between the continental slope and the Gulf Stream east of 66°W were represented by 4 or 5 cohorts. Each next cohort with the modal length of 25-35 mm appears at the northern edge of the

Gulf Stream at 20 to 30 day intervals. The rate of linear growth of the squids in cohorts during the period preceeding their movement onto the shelf is 1 mm per day on the average. Daily growth rate (DGR) of squids measuring 15 to 120 mm decreases from 12.8 to 2,3% during this period. The squids move to the shelf waters of Georges Bank, Nova Scotia and GNB at 100-130 mm ML. The time, when numerous enough cohorts appear above the shelf, can be determined by recording the decrease of mean sizes of squids in the areas where they aggregate, and also using the method of selection of normal distributions (Harding, 1949; Cassie, 1954).

The squids in cohorts, which originated from the November to January spawning migrate to the shelf in March-May, when the euphausiid biomass is the highest there (Hollingshead and Corey, 1974; Kulka and Corey, 1978). Euphausiids are the main food item in the short fin squid ration at this stage of the ontogenesis (Squires, 1957; Ennis and Collins, 1978; Amaratunga, 1980; Froerman, 1983). Daily feeding rate (DFR) of the squids 140-160 mm in length feeding on euphausiids in May comprises 8% of the raw body weight on the arerage, and DGR is 2%. The squids in cohorts resulting from the spawning that takes place after January migrate to the shelf when the food reserve becomes poorer. In July DFR for the squids with 140-160 mm ML is 2.8%, and DGR may decrease to 0.63%. In certain cases, when the density of squids of various cohorts fluctuates from 200 to 700 thousand specimens per km^2, the cannibalism of the squids of older age cohorts (170-220mm) constitutes 21 to 99% of all the food consumed. The length of the prey squids is less than 75-80% of mantle length of the predator squids (Froerman, 1983). Therefore, during the formation of summer aggregations the squids of younger cohorts originating from the spawning that takes place after December-January suffer most. Growth rates of the squids of younger cohorts are lower, but their maturation rates exceed those of the squids of older cohorts (Rowe and Mangold, 1975). Therefore, at the end of the ontogenesis the potential fecundity of survivors of younger cohorts is lower than that of the squids originating from the November to January spawning.

Spawning migration from the feeding ground begins in October or November, when the females and males attain maturity stages III and V, respectively (Burukovsky et al., in press; Nigmatullin et al., in press). The fact that several spawning peaks occur during the fall-winter-spring period can be related to the existence on the shelf, between 40°N and GNB, of some areas of high biological productivity (Georges, Browns, Emerald, Sable Island, Banquerreau, etc.), where the squids concentrate during the feeding period, until the spawning migration begins. The comparison between time intervals at which the juvenile cohorts appear in the northern Gulf Stream edge (20-30 days) and the distance between the conventional center of the spawning ground (37°N, 75°W) and conventional centers of Georges Bank, a group of banks in Div. 4X and 4W, Banquerreau Bank and GNB gives the mean migration velocity of 11.1 miles per day. This is consistent with the communication by Dawe et al. (1981) concerning the rate of spawning migration of females from GNB area (12 miles per day).

The duration of the development of a reproductive system in females from maturity stage III to spawning can be calculated from the formula:

$$TSM = \frac{DSM}{VSM}$$

where TSM is time of spawning migration (time needed for maturation of females from stage III of gonad development to spawning);

DSM is distance of spawning migration;

VSM is velocity of spawning migration.

The same formula was used to calculate the duration of maturity stage V in males from these areas.

The analysis of interaction of abiotic factors and intra-population and ecosystem processes in space and time makes it possible to draw the principal regularity of the mechanism of macroscale fluctuations of the short fin squid abundance.

During the intensification of the Gulf Stream its northern edge shifts north-westward and approaches the spawning area.

Accordingly, the transportation of the spawning products to the north-eastern part of the distribution area increases. This provides for the increase of total potential fecundity of the population, and the optimal temperature conditions (13-22°C) in the areas, where the larvae and juveniles spawn and feed, favour the increase of the recruitment abundance.

Redistribution of the maximum abundance observed during some years in the period of feeding migrations from the southern parts of the area to the north, and the back migration for spawning at the same velocity is responsible for a gradual shift of the spawning peak to a later time. However, as it was shown above, the recruitment from cohorts of later spawning is subject to high mortality. That is, if the abundance in the north of the feeding ground rises above the average level, which corresponds to the level of balance of biological productivity in the area, biological mechanisms directing the vector of the process of abundance variation towards the mean value begin to act. During this period the action of the biological mechanism for optimization of the abundance coincides with the return of the Gulf Stream to the mean long term position, while further deviation of the stream to the south-east from the mean reduces the transportation of the spawning products to the areas of Georges Bank, Nova Scotia and GNB. As a result, the total fecundity of the population decreases , but the time of peak spawning is reverted to the optimum period. The abundance in the feeding (peripheral) area of the distribution range (Nova Scotia, GNB) decreases to the mean value and lower, and in the reproductive (central) area it restores the mean optimum (supporting) level. Over the period from 1960 to 1982 the deviation of the Gulf Stream from the mean long term value both in north-west and south-east directions persisted for 5-6 years. The periods of high and low (unstable) squid abundance in the areas of Nova Scotia and GNB were of the same duration. The inertia of the mechanism of interaction of biotic and abiotic parameters changing the direction of the vector of abundance variation is 3years. The abundance fluctuations are most clearly pronounced in the periphery of the species distribution range (GNB area). In the center of the area (Mid-Atlantic Bight), where the feeding and reproductive zones are in immediate proximity, the year- to-year amplitude of abundance fluctuations is not wide, because of high stability in securing the recruitment during the unfavourable years of high abundance. Durability of both the periods of varying abundance and the period of inertia, in the course of which the direction of the vector of abundance variation changes, depends on the state of the Gulf Stream - Labrador system within the range of the long term variability (11-12 years). Protracted position of the Gulf Stream in the extreme north-western part of the area would change the recurrence of abundance fluctuations. In such a case short periods (2-3 years) of low abundance would correspond to 5-6 year long period of high abundance.