

## SOME PROBLEMS OF REPRODUCTIVE BIOLOGY OF OCEANIC AND NERITIC TUNAS OF THE TROPICAL ATLANTIC

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## SUMMARY

The duration of the individual reproductive period does not exceed a half year in all the studied species. Relatively synchronous maturation of individuals of a single local grouping may be noted. The duration of the mass spawning is comparable with that of the individual reproductive periods. The "year-round" pattern of the bigeye and yellowfin tuna spawning results from combining the reproductive seasons of the groupings from the Northern and Southern Hemispheres where the sexual cycles are in opposite phase. Both species are represented in the tropical Atlantic by at least two independent groupings: of the Northern and Southern Hemispheres. There exist marked differences in reproductive characteristics of the representatives of the neritic and oceanic tuna groups. In this context the neritic-oceanic yellowfin tuna occupy an intermediate position.

## RESUME

La durée de la période individuelle de reproduction ne dépasse pas six mois pour toutes les espèces étudiées. On a pu observer une maturation relativement synchrone chez les individus d'une même concentration locale. La durée de la ponte de masse est comparable à celle des périodes individuelles de reproduction. Les caractéristiques de la ponte du thon obèse et de l'albacore au fil de l'année ont été obtenues en combinant les saisons de reproduction des groupes des deux hémisphères,

dont les cycles sexuels sont en opposition de phase. Ces deux espèces sont représentées dans l'Atlantique tropical par au moins deux groupes indépendants: hémisphère nord et hémisphère sud. Il existe des différences accusées entre les caractéristiques de reproduction des groupes océaniques et celles des groupes de la plate-forme continentale. L'albacore, qui est méritico-océanique, représente à cet égard un cas intermédiaire.

## RESUMEN

La duración del periodo reproductivo individual, no excede de medio año en todas las especies estudiadas. Se debe anotar, la maduración relativamente sincronizada de individuos de un grupo individual local. Es comparable la duración de gran cantidad de desove, con los periodos individuales reproductivos. La "Ronda anual" de distribución de los resultados del desove del patudo y rabíl, resulta de combinar las estaciones de reproducción de los grupos del hemisferio Norte y Sur, donde los ciclos sexuales están en fase opuesta.

Ambas especies están representadas al menos en el Atlántico Tropical en dos grupos independientes: Norte y Sur del hemisferio. Allí existen marcadas diferencias en las características reproductivas de los grupos representativos del nerítico y oceánico. En este contexto, el rabíl nerítico-oceánico, ocupa una posición inmediata.

## Abstract

The paper reviews reproductive peculiarities of neritic, neritic-oceanic and oceanic tunas, Euthynnus alleteratus, Auxis thazard, Auxis rochei, Katsuwonus pelamis, Thunnus obesus, Thunnus albacares of the tropical Atlantic.

The results of histological and variation-statistical analyses of the ovaries ascertain the continuous maturation type and interrupted-asynchronous pattern of vitellogenesis. Different intermission rates are noted for the representatives of various ecological groups. The approximate values of the portion numbers, intervals between their spawning and duration of individual reproductive periods are given. The areas of bigeye tuna mass spawning are located and their relation to productive zones of the northern and southern tropical cyclonic gyres is suggested. The sexual cycles of reproductive groupings from both spawning grounds are proved to be in phase opposition. The presence of at least two independent bigeye and yellowfin tuna groupings is suggested in the Northern and Southern Hemispheres of the tropical Atlantic.

It is assumed that the differences observed between the fecundity and spawning pattern of neritic and oceanic tuna species can be attributed to different nature of productive zone localization - fixed in the neritic and of probability nature in the oceanic waters.

Reproduction of tunas in the Atlantic Ocean remains the least investigated aspect of their biology. The notion of the year-round tuna spawning in the equatorial waters and reduced spawning period along both peripheries of the tropical zone is the one most widely spread (Parin, 1968; Zharov, 1970; Shubnikov, 1974; Chur, 1977). The extent to which the year-round spawning is stipulated by the duration of the individual reproductive periods, asynchronous sexual maturation of the individuals or, after all, by different spawning times of various interchanging reproductive groupings is unknown. The hypotheses relative to the vitellogenesis nature, portion numbers, individual spawning duration and degree of identity or difference between the reproductive physiology of the neritic "smaller" and oceanic "larger" tunas are contradictory (Zharov, 1970, 1973; Bataljants, 1975, 1976; Alekseeva, 1976 a, b, c; Alekseeva and Alekseev, 1976).

"Smaller" tunas, Euthynnus alleteratus, Auxis thazard, A. rochei; Katsuwonus pelamis and "larger" tunas, Thunnus obesus and Thunnus albacares have been studied based on the material collected for the 1969 to 1977 period. A total of 380 ovaries was examined and in 98 the size distribution of the oocytes of trophoplasmatic growth was determined; the maturity coefficients were estimated in 114 sexually mature females and the sexual cycles reconstructed from 11 thous. visual determinations of the female maturity stages. The sampling areas are shown in fig.1.

From the histological and variation-statistical analyses of the ovaries at different maturity stages (immature - II; maturing -

III; mature - IV, IV-V, VI-IV; ripe - V; spent - VI) the following conclusion is drawn: the continuous (according to Cötting's classification, 1961) ovary maturation type is characteristic of all the species studied. The fund of the oocytes of trophoplasmatic growth (expenditure fund) is replenished with the spawning of ripe eggs at the expense of the oocytes of protoplasmatic growth (reserve fund). The replenishment of the expenditure fund ceases in a certain moment during the spawning and the portion volume relative to the expenditure fund increases by the end of the spawning.

It is assumed that the maximum volume of the expenditure fund replenishment achieved during the spawning does not exceed its pre-spawning volume. The maximum absolute individual fecundity is, therefore, within the range of doubled number of oocytes of trophoplasmatic growth available prior to spawning. The expenditure fund is not utilized completely. There is always a considerable number of oocytes in early vitellogenesis phases available in the ovaries of spent females.

The trophoplasmatic growth period is subdivided into 4 phases: 1 - primary fat deposition, 2 - deposition of small yolk granules; 3 - intensive trophoplasmatic growth, 4 - yolk filled oocyte (oocyte of definitive size). The maturation period consists of two phases: 1 - fat confluence, 2 - homogenization and hydration.

The vitellogenesis of "smaller tunas" is of an interrupted-asynchronous pattern (according to B.N. Kazansky's classification, 1949). Three size groups of oocytes are distinguished in the ovaries at maturity stages IV-V: oocytes in the maturation phase 1, those closing the vitellogenesis phase 2, and oocytes in the

vitellogenesis phase 1 and at the beginning of phase 2 (fig. 2). The first two size groups correspond to volumes. The portion volume averages 28% of the expenditure fund available in "smaller" tunas. With regard for expected replenishment of the expenditure fund, the number of portions does not exceed 7-8 for "smaller" tunas. The oogenesis, size distribution of oocytes of trophoplasmatic growth and their change during ripening and spawning are identical in "smaller" tunas (fig. 2). The interrupted pattern of vitellogenesis is less pronounced in bigeye tuna. The portion volume averages 7% of the expenditure fund for this species. Under the above-mentioned conditions the number of portions spawned by bigeye tuna may exceed 20. The number of portions calculated for all the species is tentative and may be of interest in the context of the order of magnitudes. Actually, the portion number depends on the condition of a certain individual and availability of the complex of spawning conditions.

A question of the intervals between egg-layings is the one of great importance. Immediately after laying the next egg portion the oocytes of older generation of "smaller" tunas are in the completed vitellogenesis phase 2, and about 65% oocytes are of definitive diameter. In this case, the intervals between egg-layings of more than 3-4 weeks may be suggested based on the tentative values of the vitellogenesis successive phase changing rate within the annual range of the sexual cycle. The duration of the individual reproduction season, therefore, may fluctuate between 4 and 6 months. The maturation of the individuals in each of 3 studied areas (fig. 1) is relatively synchronous. Therefore, the spawning duration of a definite grouping may be comp-

ared to the duration of the individual reproductive period. After laying the next egg portion, the oocytes of older generation of "larger" tunas are in the vitellogenesis phase 3, and about 85% oocytes are <sup>of</sup> definitive diameter. In this case the intervals between egg-layings are likely to be considerably shorter than in "smaller" tunas. Provided that their duration is 10 days, the individual duration of the reproductive period may be of the order of six months.

Yellowfin tuna may be ranked among "smaller" tunas due to the degree of size isolation of oocyte generations (fig. 2). By the oocyte condition of two older generations it is closer to bigeye tuna, while by the relative portion volume it occupies the intermediate position. Immediately after laying the next egg portion, the oocytes of older generations are in the vitellogenesis phase 3, like in bigeye tuna, and about 80% oocytes are of definitive diameter. The intervals between egg-laying, therefore, also may be shorter than those in "smaller" tunas. The portion volume relative to the expenditure fund amounts to about 16% and under the conditions assumed for bigeye tuna the portion number may be 10-12, while the individual duration of the spawning period amounts to 3-4 months on the average.

The sexual cycles of little tunny, frigate and bullet mackerels are similar in each of the three investigated areas. Off Freetown their spawning begins in February and comes to the end in summer. In October the females with the ovaries at the maturity stage II and at the beginning of stage III prevail. Skipjack spawn in this area beginning from April. The mass spawning of "smaller" tunas (except for skipjack) off Pointe Noire takes

place in the summer - fall period of the Southern Hemisphere, that is from January to June. In August-November the specimens with the immature gonads are predominant. Skipjack begin spawning in November or December. The starting-point of skipjack spawning may differ by year. In December 1973 and 1977 along with the dominant maturing females the spawning individuals were recorded, and in December 1976 the ovaries of the majority of the fish were at stage II and at the beginning of stage III. The spawning of the skipjack in both areas was shorter and undoubtedly timed to warmer periods.

Around Fernando Poo, in little tunny, frigate and bullet mackerels the maturity stage III gonads prevailed in April, the mass spawning was observed in June, and as soon as in October the gonads of the majority of the fish were at stage II. The spawning is likely to occur there in the spring-summer period. Skipjack was represented by spent individuals in April-July and by the females at maturity stage II and at the beginning of stage III in October. The spawning evidently took place in the winter-spring period. Larval skipjack was observed in that area in January-March (Nisikawa, Kikawa and Ueyanagi, 1978).

Two areas of mass spawning of bigeye tunas were established: the open Gulf of Guinea and the Western part of the Tropical Atlantic (fig. 1). In both areas the spawning takes place in summer time of the respective Hemisphere with the peaks in January-February for the first area and in June-July for the second one. There is a good correlation between the data of the mass spawning time and the observations on the seasonal larval distribution (Richards, 1969; Richards a. Simmons, 1974; Rudomiotkina,

1973). The sexual cycles of reproductive groupings in these areas are in phase opposite (fig. 3). In both areas the spawning <sup>is</sup> timed to the maximum development of the northern and southern tropical cyclonic gyral (Mazeika, 1967; Bulatov, Stepanov, 1968; Moroshkin, Bubnov, Bulatov, 1969; Mratov, 1973; Khanaichenko, 1973, 1974). Relative to gyral, both areas are shifted westwards and to the equator in the northern and southern trade wind current direction.

The distribution of the tuna commercial catches (Annual report ..., 1976) and our data indicate that both areas are the spawning grounds where tunas from vast distribution areas concentrate in the reproductive period. On termination of the spawning the concentrations disperse. The feeding and spawning grounds of the reproductive grouping are isolated in the second area and overlap partly in the first area. The vegetative region of the bigeye tuna distribution area extends towards the productive zones of the south-boreal and north-tropical waters, to the areas with the seasonal hydrological and production phenomenon proceeding in the phase opposite, which suggests the intraspecific differentiation. This species is probably represented in the Atlantic Ocean by at least two groupings: of the Northern and Southern Hemispheres. Off the northern coast of the Gulf of Guinea, westward of the zero meridian, the spawning of a grouping with the sexual cycle characteristic of the Northern Hemisphere was observed in summer, and the larvae were found there in August-October (Richards a. Simmons, 1971). Thus, the reproductive regions of both groupings overlap partly. However, since their sexual cycles are in phase opposite and the spawning occurs during the opposite

calendar time, they may be more or less or even quite independent in terms of reproduction.

The distribution of the yellowfin tuna females with the immature, maturing and ripe gonads was not uniform within the investigated area (fig. 1). In the open Gulf of Guinea (area I, fig. 1) the relative number of maturing individuals was high over the whole observation period at relatively low number of females with ripe gonads (fig. 3). In January-April in the inshore regions of the Gulf of Guinea westward of 15°W and southward to 13°S the mature females predominated (fig. 3). With maturation, yellowfin tunas seem to migrate from the open part of the Gulf to the inshore waters. The spawning usually takes place in the areas of the coastal upwelling. Less intensive spawning in the open regions is mainly related to the equatorial zone between 3°N and 3°S.

In August-October, off the northern coast of the Gulf of Guinea (area III, fig. 1) a grouping of yellowfin tuna with the sexual cycle oriented to the summer-fall spawning (fig. 3) was fished. In August-October, to the north of 3°N a great number of larvae was observed, however, they were not recorded in more southern regions. It is probable that like in case with bigeye tuna, yellowfin tunas with the sexual cycle of the Northern Hemisphere spawn in summer off the northern coast of the Gulf of Guinea. It means that yellowfin tunas of the eastern part of the Atlantic Ocean may be also subdivided into at least 2 groupings: of the Northern and Southern Hemispheres.

The reproductive physiology of the neritic "smaller" and oceanic "larger" tunas differs markedly. Bigeye tuna spawns cons-

iderably larger number of egg portions of relatively smaller volume at significantly shorter intervals than the neritic species. The mean values of the maturity coefficients of females at stage IV are close for all species (2.8-3.4). Therefore, specific expenses for egg production may be compared and it follows that larger absolute sizes of bigeye tuna provide considerably higher absolute individual fecundity. The "worth" of an individual given in the egg number is significantly higher for the oceanic bigeye tuna. Considering more limited species diversity and lesser density of fish aggregations in the tropical oceanic epipelagic waters compared with the pelagic waters of the neritic zone, the higher bigeye tuna mortality at early ontogenetic stages may be hardly explained by direct influence of the biotic factors. It rather results from the indirect annihilation through the food supply. The neritic zone differs from the oceanic epipelagic region in the main in fixed localization of the productive (upwelling) areas, which can be attributed to geomorphological factors. The definite productive "patches" within the areas of the oceanic upwellings, on the contrary, have no fixed localization. They are formed in any given point of the area in probability order and their "life duration" cannot be foreseen. The oceanic epipelagic regions, therefore, as the environment for reproduction of the species spawning in the pelagic waters differ from the neritic pelagic waters in principle. Larger sizes of the oceanic tunas can be related not only to advantages they offer to predatory necters, but also to the necessity of increasing the individual fecundity to compensate for higher mortality on their planktonic ontogenetic

stages. The ability to spawn large number of portions at short intervals combined with the outstanding mobility allow the oceanic bigeye tuna to employ the vast areas for intensive reproduction. "Smaller" tunas possess no such advantages; their reproduction occurs within the limit of the neritic zone or identical areas of topogenous upwellings around the archipelagos and banks. According to reproductive characteristics considered above the neritic-oceanic yellowfin tuna occupies an intermediate position between the neritic and oceanic species. On these grounds we may suggest that the differences in the reproductive physiology of bigeye and "smaller" tunas result rather from ecological than systematic differences between these species.

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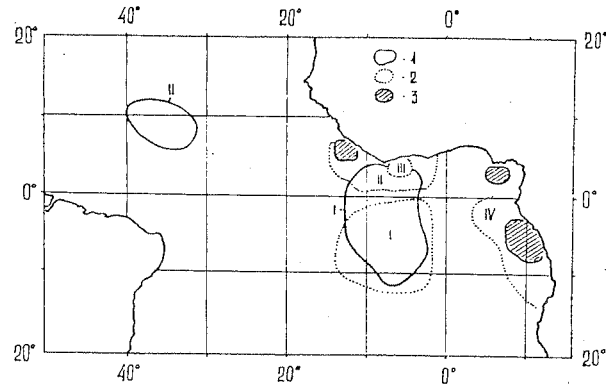


Fig. 1. The areas of the bigeye (1), yellowfin (2) and "smaller" tuna investigations.

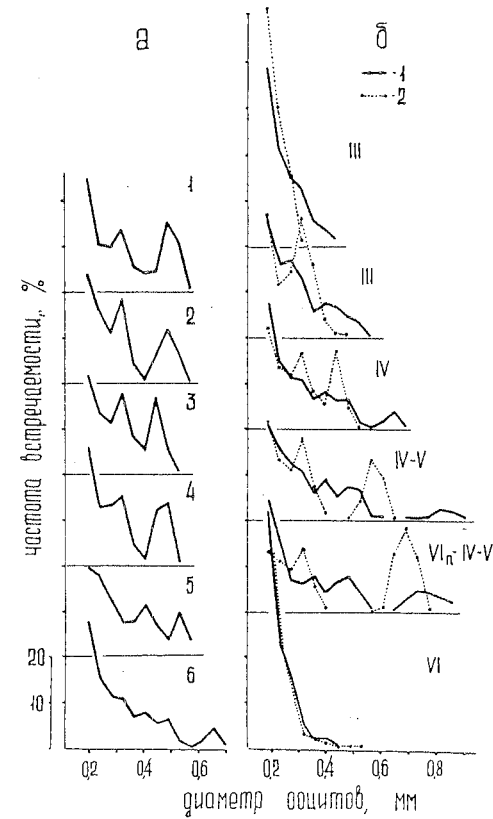


Fig. 2. Size distributions of the oocytes of trophoplasmatic growth:

a) in maturity stage IV-I ovaries

1 - frigate mackerel, 2 - bullet mackerel, 3 - little tunny, 4 - skipjack, 5 - yellowfin tuna, 6 - bigeye tuna.

b) in ripening (III), mature (IV, IV-V, VI-IV) and spent (VI) ovaries

1 - bigeye tuna, 2 - little tunny.

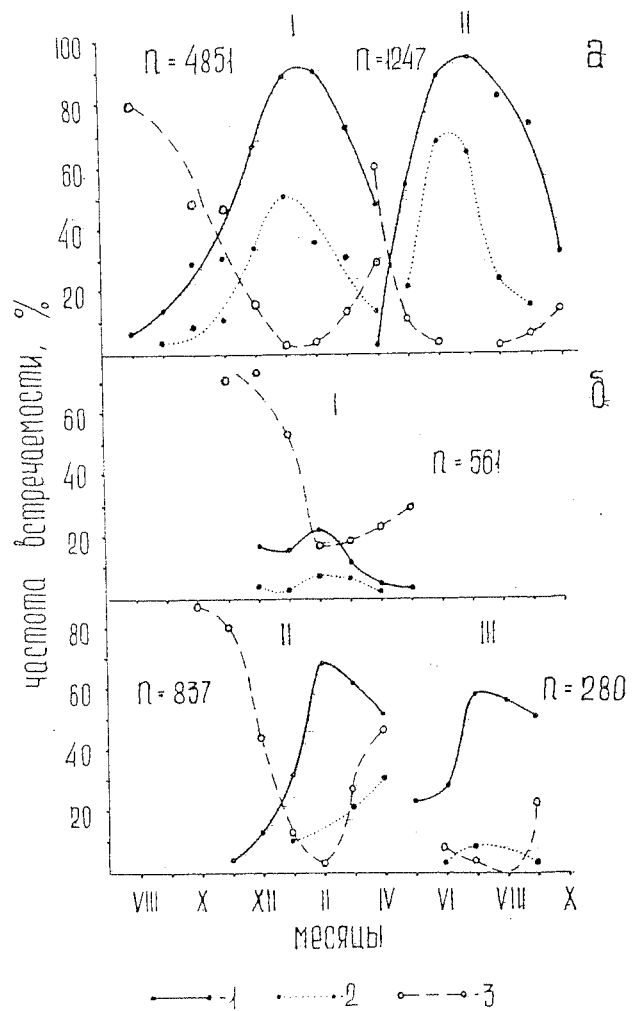


Fig. 3 . Maturity stages of the female ovaries for bigeye (a) and yellowfin (b) tunas. Investigation areas are indicated numerals (see fig. 1)

Maturity stages:

1 - IV, IV-V, VI-IV; 2 - IV-V, V; 3 - II, VI.