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MACROSCALE WATER CIRCULATION, ONTOGENETIC GEOGRAPHICAL
DIFFERENTIATION AND POPULATION STRUCTURE OF ALPONCINO,
BERIX SPLENDENS LOWE, IN THE ATLANTIC OCEAN

Abstract

Based on the analyses of spatial differentiation of alfonsino by size-age composition, physiological condition and frequency of locus Est - II a hypothesis of life cycle, functional structure of the distribution area and population structure is suggested. According to this theory, there exist at least three populations in the Atlantic Ocean localized in macroscale, subtropical and tropical cyclonic eddies. Areas, where these populations range, are subdivided into vegetative and reproduction regions related to geographically isolated thalassobathyal and benthopelagial zones of continental slopes. Certain stages of the life cycle are correlated with definite elements of macrocirculation systems. The currents which divide adjacent eddies serve as effective interpopulation barriers.

Résumé

L'analyse de la différenciation spatiale du beryx d'après sa composition taille-âge, son état physiologique et les fréquences des allèles du locus Est-II a permis de formuler l'hypothèse du cycle vital, de la structure fonctionnelle de l'aire de répartition et de la structure de population selon laquelle il existe en océan Atlantique au moins trois populations localisées dans les macrotourbillons, les tourbillons subtropicaux et tropicaux cycloniques. Les aires de répartition des populations sont divisées en aires végétative et reproductive liées aux secteurs géographiques limités de la thalassobathyale et la benthopélagiale des talus continentaux. Quelques stades du cycle vital liés aux éléments de systèmes de macrocirculation et divisant des tourbillons voisins représentent les barrières effectives qui séparent les populations.

Introduction

An attempt was made to formulate a hypothesis of functional structure of the distribution area, life cycle and population structure of alfoncino *Beryx splendens* Lowe 1833 from a vast area of the Atlantic Ocean between the forties of the northern and southern latitudes with inadequate data available. All principal theses of the hypothesis can be verified in specific areas, at definite time periods using definite methods. The present paper is aimed at the development of the general approach for planning a more detailed research of the species in question for assessment of its prospective utilization and regulation measures.

Materials and methods

The materials were collected in 1976-1979 and in 1984 in Sub-areas I-III (fig. 1). Indications of the obtained data are presented in the text. Reproductive cycles were constructed from the data of visual examination of maturity stages of gonads of 38.3 thousand specimens and histological examination of ovaries from 160 females 21-45 cm in length (fork length). Relative and absolute volumes of portions were determined by hydratased but yet not ovulated oocytes (IY-I maturity stages). The patterns of formation of the expense fund and spawning type were determined from diameters and number of oocytes with yolk in the batches of the ovaries at maturity stages III, IV, IY-I, II-II and II. Electrophoretic fractionation of muscle esterases of 3 353 sp. was made by Titova (1981). G - criterium of modified χ^2 - test was used as a criterium of conformity in a repeated analysis of electrophoretic data; heterogeneity of samples and their aggregates were estimated using the arcsine transformation (Zhivotovsky, 1983).

Results and discussion

Range. Alfonsino has a wide distribution range in the tropical and subtropical waters of the World Ocean (references in Busachin, 1982). The species is not numerous in the Atlantic Ocean between 65°N and 40°S, to the north of 40°N and in the area of continental slopes of the West Atlantic, between Nova Scotia and southern Brasil. It is common above the continental slopes in the East Atlantic, and is abundant in the Morocco-Mauritania and Namibia-SAR regions, forming in some years commercial aggregations there and above the shelf. In the open Atlantic waters it generally occurs between 52°N and 36°S. The species is abundant above the slopes of island bases and elevations around Madeira, the Azores and Canary Islands, Atlantic Corner Seamounts, Cabo Verde Isles, Sierra-Leone elevation, on the Vavilov Ridge, around Saint Helena Island, on Ridge of Whales, in the area of Tristan da Cunha and on Rio Grande elevation. In some of the above-mentioned areas commercial aggregations are formed (Polonsky, 1979).

Reproduction. Partial spawning, number of portions approximately 10-12. Spawning evidently occurs in four-day intervals. High fecundity. Number of oocytes with yolk in ovaries of prespawning females (stage II) 40-45 cm in length is 0.8-2.3 mill. Ovulated intraovarian eggs preserved in 4% formalin are 1.2 mm in diameter on average (Alekseeva, 1983). No descriptions of drifting eggs and larvae exist. Larvae are evidently epipelagic due to small size of the eggs. Fry 4-10 cm in length are common in the epipelagic zone above the ocean depths in the area of the Angola hollow and above the continental slopes of the Southeast Atlantic. In September-October 1983 the young of 3-10 cm were caught in the layers 600-0 and 300-0 above the Atlantic Corner Seamounts (Sher-

stjukov, Noskov, in press). The spawning occurs in a warm season, with the peak in July-August in the northern hemisphere (Atlantic Corner Seamounts), and in January-March in the southern hemisphere (Vavilov Ridge) (Alekseeva, Alekseev, 1964; Alekseeva, 1983).

Ontogenetic spatial differentiation. Both in the northern and southern hemispheres, in the areas of massive distribution, a distinct geographical differentiation of alfonsino by size-age composition (figs. 1,2, table 1) and by mature to immature fish ratio has been observed during several years of research.

Above the Atlantic Corner Seamounts (area I, fig. 1), only mature alfonsino of older age groups were caught: prespawning and spawning in April-August and maturing in December. Massive spawning was recorded in July-August. Around the Azores (area II), immature specimens predominated in February-June. The catches taken off the Northwest African coast (area III) were represented exclusively by immature fish (Domanovsky, 1974).

On the Vavilov Ridge (area IV), only mature alfonsino were caught: spawning and postspawning in April-June and maturing and prespawning in September-October. Off the Southwest African coast (area V) and in the northern part of the Ridge of Whales (area VI), the bulk of the catches consisted mainly of immature fish with the mature specimens represented by first maturing fish. Immature fish also predominated in the southern part of the Ridge of Whales (area VII). The maturing fish is supposed to migrate from that area (Alekseeva, Alekseev, 1984; Alekseeva, 1983).

Thus, both in the northern and southern hemispheres the areas inhabited exclusively by mature specimens (I and IV), mainly by immature (II, VII) and only by immature (III, V, VI) can be dist-

inguished. The distribution range of alfoncino in the Atlantic is likely to be divided into geographically isolated and functionally differing regions. Spatial differentiation by size-age composition and physiological condition is similar in both hemispheres, therefore, it can be considered as a species-specific type of functional structure of the area. These facts are fundamental in definition of the hypothesis of population structure.

Population structure. Hypothesis. Evidently, none of the considered areas, each taken separately, is a functionally ideal population area, but a part of such. Considerable spatial disconnection between even geographically close habitats of immature and reproductive contingents is indicative of massive long distance migrations, passive and active, performed by the fish. In both hemispheres, in definite areas, such ontogenetic groups predominate which are either absent from the adjacent areas or represented very poorly. When unified (I-III; IIY-II), they become functionally important areas with reproductive and vegetative zones, involving all stages of the life cycle (Alekseev, 1984). On these grounds, the availability of at least two populations can be suggested in the two hemispheres.

Verification of the hypothesis. The analysis of geographical differentiation of alfoncino in frequencies of A and C alleles of the five-allele locus Est-IX A'ANCD showed the following results. The distribution of phenotypes in all 22 samples was consistent with the Hardy-Weinberg ratio. Differences between samples from each separate area are statistically insignificant. Samples from areas I+II, like those from areas IIY-II, are genetically homogeneous. Therefore, the groups of areas I+II may belong to a single population, like the groups of areas IIY+II.

Sum of samples from areas I+II does not differ in frequency of A in samples from areas II+VI, but positively differs in frequency of C (fig. 3). Therefore, the groups occurring in the northern and southern hemispheres belong to different populations. Sum of samples from area III positively differs in frequencies of both genes from samples obtained in areas I+II and II+VI. Thus, the Ridge of Whales alfoncino are represented by two populations, and the studied regions of the Atlantic are inhabited by at least three genetically varying populations. The results of the genetic-biochemical research are consistent with the preliminary hypothesis of the population structure. However, although a suggestion on the identity of populations in areas I+II and II+VI is relatively well argumented by the fact of the ontogenetic differentiation alone, the Ridge of Whales alfoncino population cannot be divided on the same basis. Genetic studies are decisive in this case.

Macroscale water circulation and functional structure of the area. The scheme of population differentiation and functional structure of the areas is shown in fig. 1. The North Atlantic population inhabits the North Subtropical Eddy (NSE). Epipelagic eggs, larvae and fry drift from the reproductive zone (I) to the vegetative zone (II and III) located in the waters of the northern periphery of NSE, where southern branches of the North Atlantic Current pass. The youngs settle on the elevations in a more productive eastern part of the eddy. The appearance of immature alfoncino on the continental slopes and on the Morocco-Mauritanian shelf in large number is related to active migration of the fish across the Canary Current. Since in the areas of occurrence of the immature alfoncino (II, III, IV, VI) the specimens below 14-15 cm in length are absent from the catches, it

can be suggested that the fish stay in the open paleogial untill they attain this length. On maturing, alfonsino perform lengthy migrations to the reproductive zone. Mature specimens constantly stay in the reproductive zone.

In the anticyclonic system, the circulation has a "centripetal" constituent (Stepanov, 1974), therefore, the drift of planktonic stages outside the limits of NSR being a usual thing does not become a large-scale phenomenon. To the west of the Gulf Stream and to the north of the North Atlantic Current alfonsino are scanty or rare. These, evidently, are expatriation areas.

At least two populations occur in the southern hemisphere. One of them is basically distributed in the South Tropical Cyclonic Eddy (STCE). The spawning on the Vavilov Ridge (II) takes place during the period of seasonal intensification of the Angolan Current (Khanaichenko, 1974; Khlystov, 1977). Planktonic stages drift in the western periphery of the Angolan Current. Due to predomination of the "centrifugal" constituent of the cyclonic eddy, the youngs find themselves on the continental slopes of the Namibian area and on the northern part of the Ridge of Whales. The drift to its southern part is barred by the Benguela Current. Maturing specimens migrate from areas I, II to the reproductive zone, possibly, along with the passing waters of the eastern periphery of the Benguela Current.

The southern part of the Ridge of Whales is inhabited by the other population differing genetically from the neighbouring population of STCE. A boundary between the distribution of high and low values of allele frequencies passes at approximately 24°-26°S, i.e. it coincides with the middle position of the main flow

of the Benguela Current. In this narrow frontier zone, components of the neighbouring populations may overlap in space (fig. 4) as a result of drift fluctuation or active migrations. The availability of the boundary dividing the Ridge of Whales is also confirmed by faunistic differences between its northern part with the adjacent continental slope and the southern part (Burukovsky, Romensky, 1982; Pekhorukov, 1980).

Little can be said about the functional structure of the distribution range of the southern Ridge of Whales population. Since immature specimens predominate there, it can be considered as a vegetative zone of the population range, and the reproductive zone is located more to the south-west, possibly, in the area of Tristan da Cunha. On the Ridge of Whales the proportion of mature specimens increases from 24° to 32°S. With the available data, even a possible correlation between the groups of alfoncino of the Ridge of Whales and the Rio Grande area cannot be flatly denied. However it is more probable that the alfoncino population of the South Subtropical Eddy (SSE) is divided into two populations which occupy the eastern and western parts: area III-Tristan da Cunha, and the areas of Trindadi and Martin Vaz rocks-Rio Grande elevation (fig. 1). Alternative hypotheses of the unity or differentiation of the SSE alfoncino population can be easily verified by the genetic-biochemical examination of the samples from the eastern and western parts of the eddy.

Biotopic classification and approach to stock assessment.

The suggested hypothesis has a number of applied aspects. We shall consider one related to a general approach to stock assessment.

All studied areas (I-III) are characterized by "disappearance" and "reappearance" of alfoncino as well as by a marked change of

the size composition and physiological condition of the fish in the catches taken from separate elevations. These facts are indicative of fast movements of various size-age groups between the mounts within the limits of separate elevations. Appearance of numerous alfonsino populations off the northwest African coast is another evidence of active lengthy migrations. After all, the fact of macroscale geographical ontogenetic differentiation is an indisputable argument confirming the existence of lengthy migrations across the open pelagial. The migration way of first maturing specimens exceeds 1000 miles in NSE and 700 miles in SSE, therefore, at least this ontogenetic group involving the fish of four age classes, stays in the open pelagial for a long time.

Alfonsino cannot be definitely and without doubt attributed to bathopelagic (thalassobathial) species.

The open pelagial is inhabited by the fry, it is crossed by the feeding fish migrating between separate mounts and first maturing specimens performing lengthy migrations. The pelagial between the seamounts can be considered as at least a specific transit region. Besides, it cannot be denied that usually alfonsino are scattered or aggregated in the open pelagial while in the thalassobathial and bathopelagic along the continental slopes they concentrate where assemblages of food organisms occur. Typically, oceanic species also form similar concentrations in the areas of undersea mounts (Parin, Prutko, 1985; Kukuev, 1982). If alfonsino settle the open pelagial of macroscale eddies (even if with low density), their stock size is considerably larger than the instantaneous biomass on the undersea mounts accessible to trawls or to hydroacoustic instruments used for its assessment.

Conclusions

Alfoncino in the Atlantic Ocean are subdivided into at least three genetically differing populations.

Their distribution areas occupy macroscale eddies: North Subtropical, South Tropical Cyclonic and South Subtropical (probably two populations: in the eastern and western parts of SSE). The availability of another population in the North Tropical Cyclonic Eddy with the reproductive zone along the Sierra-Leone elevation and the vegetative zone at Cabo Verde Islands can be suggested.

The habitats of alfoncino in NSE and STCE are similarly subdivided into geographically isolated reproductive and vegetative zones. Spatial differentiation of the population is of the ontogenetic character.

Existence at certain stages of the life cycle is correlated with definite elements of microcirculation systems.

Functional structure of the distribution area is determined by the position of the reproductive zone, orientation and extent of the drift of the planktonic stages.

Macroscale geographic ontogenetic differentiation of alfoncino in NSE and STCE proves the fact of lengthy migrations.

Main currents dividing the adjacent macroscale eddies are effective interpopulation barriers.

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Table 1

Size and age characteristics of alfonsino and
number of examined specimens (n) by areas I-III (fig. 1,2)

Area	length, cm		mean age, years	n
	range	mean		
I	28 - 47	36,72	7,41	24589
II	15 - 45	23,67	3,41	25028
III	15 - 33	23,04	3,02	706
IV	19 - 42	31,60	5,96	1618
V	14 - 28	20,00	1,96	753
VI	15 - 33	22,69	2,85	4398
VII	15 - 37	22,14	3,17	27877

Figure legends

1



2

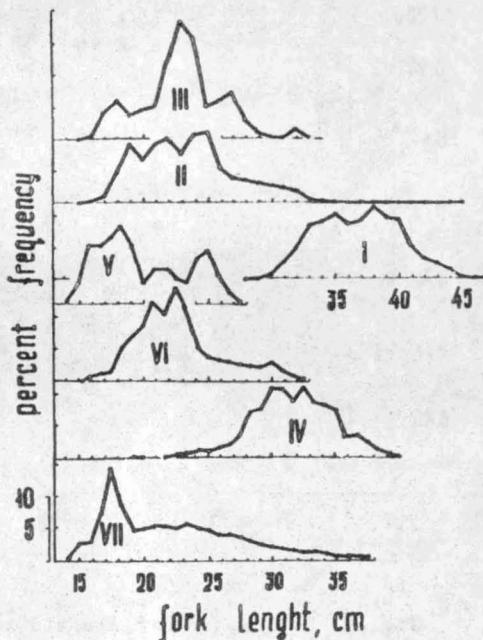


Fig. 1. A scheme of population differentiation and functional structure of distribution areas of alfonsino in the Atlantic

Ocean. Roman numerals (I-III) denote studied areas.

1 - reproductive zones;

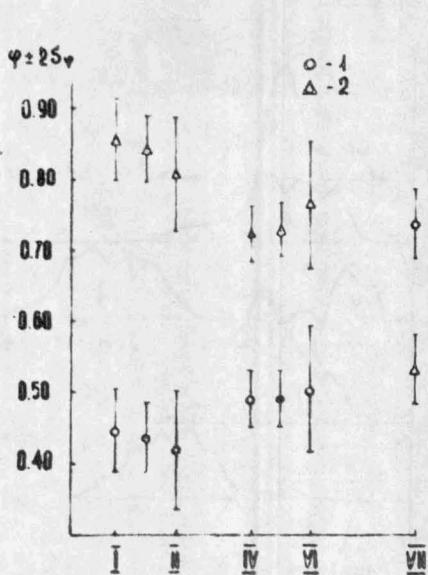
2 - vegetative zones (those not denoted by Roman numerals are hypothetic);

3 - supposed direction of drifting of planktonic stages;

4 - supposed directions of migrations of first maturing fish.

Fig. 2. Size composition of alfonsino in I-III areas (see fig. 1).

3



4

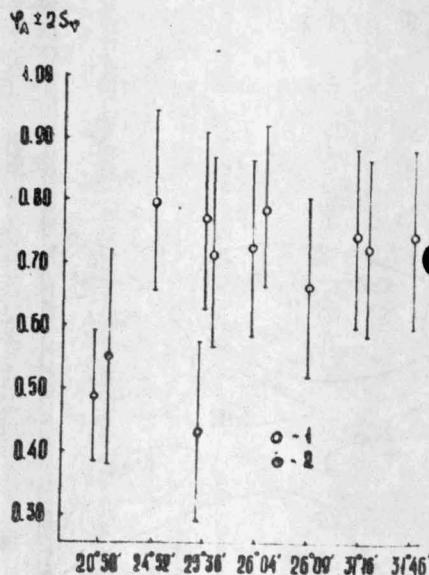


Fig. 3. Geographic differentiation of alfonsino by frequencies of A (1) and C (2) alleles. Painted marks show frequencies in sums of samples of areas (I+III) and (II+VI).

Fig. 4. Differentiation of alfonsino on the Ridge of Whales (areas II, III) by frequencies of A allele in 1977 (1) and 1978 (2).