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On the Distribution of Shrimp in West African Waters

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Abstract—About 250 shrimp species inhabit the waters of West Africa. They belong to three faunal complexes, corresponding to the following zoogeographical regions: Mediterranean–Lousitanian region (Mauritania province), West African tropical region, and Indian–West Pacific region (South African province). Boundaries between the West African tropical and adjacent regions lie in the sublittoral zone at 15°–16° N and 12°–13° S; in the outer shelf, the boundaries shift to the north and south to 21° N and 17° S, respectively. For the species of the shelf and of the continental slope, the northern boundary is situated at 26° N. The southern boundary is at about 22° S for shrimp living at the shelf border and at 26° S for shrimp of the slope. At greater depths, the tropical zoogeographic regions broaden (a phenomenon of equatofugal deepwater shift). To the south of the southern boundary and to the north of the northern boundaries of the West African tropical zoogeographical region, there are antiecotones, i.e., areas where shrimp species are scarce, their abundance is low (to total disappearance), species dominating in the persisting taxocenoses do not dominate in the adjacent regions, and endemics are absent. These zones are situated symmetrically to the equator and correspond to the increase of upwelling in summer. As a result of upwelling, in subtropical regions, there are some areas with low bottom temperatures similar to those in the temperate zone. Therefore, no tropical and subtropical species can inhabit these waters.

INTRODUCTION

During the last 45 years, the shrimp fauna of the West African waters has been investigated intensively (see below the review of principal studies). However, there is only one attempt at a biogeographic analysis of this fauna (Crosnier and Forest, 1973), made with reference to a small number of deep–water shrimp. During 30 years of investigations, I have collected rich faunistic material of shrimp from West African waters for such analysis, considered the regularities of position of zoogeographic boundaries of various bathymetric groups of shrimp, and attempted to investigate regularities of their distribution in transitional zones.

MATERIALS AND METHODS

Two kinds of data obtained by different methods are used. First of all, these are published data on the occurrence of shrimp in West African waters or on their geographical ranges. During the almost 120 years of investigations of shrimp from West African waters, about 200 studies have been published, and the most important ones should be mentioned. The fauna of shrimp of Morocco from 36° to 21°40′ N has been dealt with in several studies (Maurin, 1968; Lagardère, 1971; Abbes and Casanova, 1973; Burukovskii, 1980, 1982). The species composition and distribution of shrimp from 21°40′ to 16° N are partly described by Maurin (1968), and in more detail, by Burukovskii and Romenskii (1995). The fauna of the area from 12° to 4°10′ N is described by Holthius (1951) and Burukovskii (1988, 1989). The fauna of shrimp of the Gulf of Guinea has been poorly studied; just occurrences of some species are indicated (Forest, 1964; Le Loeuf and Intes, 1968; Crosnier, 1965; Rossignol, 1962). Crosnier and Forest (1966) describe mainly the island fauna. The areas of the shelf and continental slope from the equator to 10°–12° S have been better investigated (Holthius, 1951, 1952; Crosnier, 1969, 1972; Crosnier and Forest, 1964, 1965, 1968, 1969, 1973; Ribeiro, 1970; Burukovskii, 1978; Burukovskii and Romenskii, 1979). Occasional data on the shrimp fauna to the south of 17° S are mentioned by Barnard (1950), Lebour (1954), Grindley and Penrith (1965), and Kensley (1970) and in more detail by Kensley (1981), Burukovskii (1976, 1992), and Burukovskii and Romenskii (1979, 1980, 1985, 1989).

The aforementioned publications mention 250 shrimp species belonging to 81 genus from 23 families in the waters of West Africa between 36° N and 35° S.

The second source of data are trawl surveys. These data on species composition were used in my cited publications. In addition, analysis of the quantitative distribution of shrimp, especially in transitional zones, supplied data on another aspect of their distribution, almost disregarded in the aforementioned publications. In each area, the surveys were made according to a prescribed grid along transects located at distances of about 30 miles. The duration of trawling was 30–60 minutes. In each catch, the species composition, number, and biomass of all shrimp species were determined. The areas, depth range, and number of trawlings are indicated in Table 1.

Three methodical approaches are used in this study. The first is the analysis of range types characteristic of shrimp from West African waters. The second approach

is calculation of the position of the boundaries of species ranges on the basis that the position of geographic boundaries is "marked" by a concentration of boundaries of distribution species (Semenov, 1982; Nesis, 1982), i.e., by greater occurrence of the boundaries of species ranges in a particular region. The third approach is the analysis of shrimp distribution in the adjacent regions by the data of trawl surveys from one catch to another, which provides the possibility of investigating the distribution of shrimp near boundaries between the regions, to specify the location of the limits of ranges near them, and to determine the configuration of regional boundaries. These three approaches may be designated as macro-, meso-, and microscale analysis of shrimp distribution.

Table 1. Materials on distribution of shrimp collected during trawl surveys

Area	Number of hauls	Depth range, m
35°–28°40′ N	101	29–800
23°56′–21°00′ N	62	29–1230
20°32′–16°06′ N	280	18–857
11°56′–10°45′ N	36	13–735
8°59′–4°10′ N	117	13–805
2°32′ N–11°47′ S	168	22–1160
17°00′–34°00′ S	245	100–1200
Total	1009	13–1230

RESULTS

Geographic Distribution of Shrimp in West African Waters

Subdividing 250 species of shrimp from the investigated region into groups with identical range types (Tolmachev, 1962), it was revealed that Semenov's approach (1972, 1973) cannot be fully applied to them, as the number of alpha-regions becomes almost equal to the number of shrimp species occurring off West Africa. This is unavoidable if a comparatively low number of species of the same taxon is used. Another approach—specifying range types without considering shrimp distribution beyond a particular region—was found to be inapplicable in view of the necessity of taking into account whether a certain species occurs beyond West African waters, and if yes, then where.

The identified shrimp groups thus become geographic elements of the fauna (Alekhin, 1944; Beklemishev, 1967, 1969; Zezina, 1970; Semenov, 1973). In this way, the lack of information on many shrimp species, known only from occasional findings, may be neglected, and the zoogeographic region may be taken as the smallest unit of regionalization. Thus, four groups of range types were distinguished.

(1) Ranges of species endemic for a certain zoogeographic region (the species whose distribution is limited to a certain zoogeographic region).

(2) Ranges of interregional species (species occurring in more than one zoogeographic region but within the limits of a given oceanic coast).

(3) Ranges of transoceanic species (species occurring also at the opposite coast of the ocean).

(4) Ranges of widely distributed species (comprising more than one zoogeographic region and more than one ocean).

Applying such a criterion, the following range types may be outlined for shrimp of the West African waters [regions are after Briggs (1974)].

(1) Endemics of the Mediterranean–Lousitanian zoogeographic region: species living from Southern England and Ireland to the African coast, not further south than the Cape Blanc (21° N) and in the Mediterranean Sea. 17 species.

(2) Endemics of the West African tropical zoogeographic region: species living off West Africa, not further north than 26° N and not further south than 21–22° S. 43 species.

(3) Endemics of the South African province of the Indo–West Pacific zoogeographic region, living off South Africa and penetrating to the Atlantic Ocean, not further north than 22° S. Seven species.

(4) East African species, populating the Mediterranean–Lousiatanian and West African tropical zoogeographic regions. 23 species.

(5) North–East Atlantic species distributed from Norway or the North Sea to Africa, but, at its western coast, distributed not further than Central Morocco; also the Mediterranean Sea. Seven species.

(6) Amphiatlantic species present in the East and West Atlantic. 30 species.

(7) Widely distributed species occurring in addition to the Atlantic Ocean in the Indo–West Pacific and (or) in the eastern part of the Pacific Ocean. 61 species.

(8) Island species known from the Canary Islands, Cape Verde Islands, Principe, and Sao Tome, but not from the West African coast. 13 species.

One species, *Palaemon elegans*, is known from the littoral zone from Norway to South Africa. This name may combine several species, as yet unstudied.

The distribution of 48 pelagic species whose connection with the bottom is indirect or problematic is insufficiently known and cannot therefore be attributed to any range type. Thus, the West African waters are inhabited by three faunal complexes of shrimp. In each of them, the interregional, amphiatlantic, and widely distributed species more or less prevail. The complexes differ mainly in the composition of endemics marking to what zoogeographic region each complex belongs (Briggs, 1974): Mediterranean–Lousitanian region, West African tropical region, and Indo–West Pacific region.

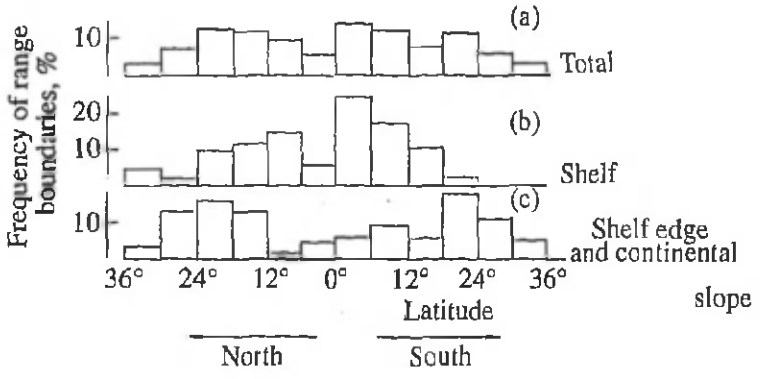

Fig. 1. Frequency distribution of shrimp range boundaries in West African waters.

Location of Zoogeographic Boundaries

In the previous section, range types were distinguished without considering distribution boundaries of particular species. For determining the location of zoogeographic boundaries, it is not important to what range type a certain species belongs. Only the position of range boundaries is important. This task is made easier by the almost meridional location of the western African coast, which makes shrimp ranges almost linear in shape, extending from north to south. The almost latitudinal position of the coast of the Gulf of Guinea is an exception, but which does not influence the results. Thus, the northernmost and southernmost limits of distribution of each species may be taken for boundaries. This does not contradict the generally accepted definitions of the range and its boundaries in bottom-dwelling and demersal species (Tolmachev, 1962; Darlington, 1966; Beklemishev, 1969; Semenov, 1972). All available materials on the distribution of shrimp were used, and many species are known from single findings, e.g., *Bythocaris cosmetops* or many Alphaeidae (Holthius, 1951; Crosnier and Forest, 1973). The island species, as well as species with range boundaries situated beyond the West African waters, are excluded. Finally, just slightly over 90 species were used in the analysis.

The great length of the coast of the African continent from north to south, over 70° by latitude, motivated selection of 6° by latitude, i.e., about 670 km, as a class interval. This is rather rough, but a greater precision is not possible at this stage of investigation due to the vague position of range boundaries in many of the species known from literature.

The frequences distribution of range boundaries for each species plotted according to these data (Figure, a) revealed two regions of concentration: 12°–24° N and 0°–12° S. There is coincidence with the boundaries of corresponding zoogeographic regions (Ekman, 1935; Balss, 1957), but the latter are excessively vague and smoothed in comparison with the published data. The vagueness of the regions where range boundaries are concentrated appears to result from summing up the data for different fauna, primarily for shrimp of the shelf, edge of the shelf, and the upper part of the continental slope.

Indeed, the frequency distributions of ranges boundaries for species belonging to each fauna separately (Fig. 1, b–c) show that the dense zones are expressed more clearly and do not coincide. In shelf shrimp, the zones of concentration of species boundaries and, hence, the boundaries between the West African tropical region and adjacent regions, are located much closer to the equator than in shrimp of the shelf edge and upper bathyal zone. In the northern hemisphere, they are located closer to the equator than in the northern hemisphere: 6°–12° N and 0°–6° S, respectively. Conversely, in more deep-water species, these boundaries are wider, reaching the limits of the tropical zone. Some concentration of the boundaries of slope species in the area of 6°–12° S is an artifact, as the area between 12° and 17° S is inaccessible for trawling and there is no information on the distribution of shrimp: here, the coastal slope is abruptly followed by a steep continental slope (Litvin and Rudenko, 1973).

Thus, the shape of the zoogeographic boundary is considerably more complex than is usually assumed.

Characteristics of Distribution of Shrimp near Zoogeographic Boundaries

Investigations on the qualitative and quantitative composition of shrimp on the shelf and the continental slope of West Africa, which covered two-thirds of their area (Burukovskii, 1978, 1980, 1982, 1989a; Burukovskii and Romenskii, 1985, 1989, 1995), revealed the zones where species composition changed abruptly, i.e. the boundaries of zoogeographic regions. They are situated in waters off the Western Sahara and Southwestern Africa.

Shrimp Fauna of Waters off the Western Sahara

The Western Sahara is the area extending from 24° to 21° N. In this area, 42 species of shrimp were found (Burukovskii, 1982), including 30 species belonging to bottom and demersal taxocenoses (Table 2).

Table 2. Distribution of shrimp in waters off West Sahara (frequency, %)

Species	23° N	22° N	21° N
Penaeopsis megalops	3.8	–	–
Aristeus antennatus	3.8	–	–
Plesionika ensis	3.8	–	–
Aristeomorpha foliacea	3.8	4.8	–
Plesiopenaeus edwardsianus	7.7	9.5	–
Processa macrophtalma	7.7	4.8	–
Hymenopenaeus debilis	11.6	14.2	–
Plesionika heterocarpus	19.3	28.5	83.5
Plesionika martia	19.3	4.8	5.8
Pasiphaea multidentata	15.4	14.2	11.1
Glyphus marsupialis	11.6	9.5	11.1
Acanthephyra pelagica	15.4	19.0	16.7
Pontocaris cataphracta	7.7	14.2	27.8
Plesionika carinata	3.8	4.8	16.7
Pontophilus gracilis	3.8	4.8	5.6
Pasiphaea tarda	–	9.5	11.1
Philocheras sculptus	–	4.8	5.6
Parapenaeus longirostris	–	4.8	15.6
Hymenopenaeus chacei	–	4.8	5.6
Solenocera membranacea	–	–	5.6
Plesionika edwardsii	–	–	5.6
Parapandalus narval	–	–	5.6
Plesionika acanthonotus	–	–	5.6
Penaeus notialis	–	–	5.6
Solenocera africana	–	–	22.2
Pasiphaea semispinosa	–	–	11.1
Aristeus varidens	–	–	11.1
Sicyonia galeata	–	–	5.6
Nematocarcinus africanus	–	–	5.6
Total number of hauls	26	21	18
Of them with shrimp	13	13	18
Frequency of shrimp in catches, %	50.0	62.0	100
Coefficient of similarity with the Morocco fauna	29.2	25.5	24.5
Coefficient of similarity with Mauritania fauna	26.8	29.3	42.9

In the northern part of this area, only 15 species were found, twice less than off Morocco (Burukovskii, 1980). In the southern part of this area, 23 species were collected, much less than the list of shrimp both of the Morocco shrimp fauna and of the Mauritanian fauna adjacent to the south (Burukovskii and Romenskii, 1995). The material was collected using identical gear and from comparable depths; thus the impoverishment of the shrimp fauna of this region is actual. Its northern and southern parts have only eight species in common, i.e., an abrupt change in the species composition occurs over no more than 120 miles.

The disappearance of some species usual for adjacent areas is accompanied by a general decrease in the frequency of shrimp in catches, especially at depths less than 200 m, where it does not surpass 28%. Deeper than 300 m, it reaches 100%. The shelf and its edge form a zone extremely impoverished in shrimp both qualitatively and quantitatively, widening from the south northward beginning at approximately 22° N. In this zone, there are either no shrimp or only single species occur in catches. The species diversity in some places drops to zero, i.e., monospecific shrimp taxocenoses are formed. The zone lacks zoogeographic individuality: only interregional (*Plesionika heterocar-*

Table 3. Distribution of shrimp in waters off South West Africa (frequency, %)

Species	16°–22° S	22°–28° S	28°–34° S
Parapenaeus longirostris	9.6	–	–
Aristeus varidens	11.5	–	–
Nematocarcinus africanus	5.8	–	–
Plesionika heterocarpus	7.7	–	–
Notostomus auriculatus	1.9	–	–
Glyphus marsupialis	1.9	–	–
Heterocarpus laevigatus	1.9	–	–
Plesiopenaeus edwardsianus	1.9	–	–
Plesionika carinata	3.8	7.3	–
Plesionika acanthonotus	3.8	9.7	–
Pasiphaea semispinosa	1.9	2.4	–
Acanthephyra pelagica	3.8	2.4	5.6
Funchalia woodwardi	–	7.3	39.0
Merhippolyte agulhasensis	–	9.7	7.4
Haliporoides thriarthrus	–	–	5.6
Aristeomorpha foliacea	–	–	5.6
Acanthephyra eximia	–	–	5.6
Pasiphaea grandicula	–	–	11.2
Pasiphaea tarda	–	–	3.2
Pasiphaea diaphana	–	–	5.6
Nematocarcinus longirostris	–	–	7.4
Pkesionika martia	–	–	29.5
Plesiopenaeus nitidus	–	–	7.4
Pontophilus gracilis	–	–	3.7
Hauls with shrimp	17	13	28
Total number of hauls	52	41	54
Frequency of shrimp	32.6	31.6	50.9
Coefficient of similarity with the fauna of tropical West Africa	26.3	7.7	6.5

pus and *Processa macrophthalma*) or widely distributed species (*Pontocaris cataphracta*) are present here. Outside this zone, the endemics of the Mediterranean–Lousitanian region (on the shelf) and of the West African tropical region (in the upper part of the continental slope) are present.

The boundary between two zoogeographic regions within limits of the investigated transitional zone is situated at different depths in different parts of this area: on the shelf, in its very south; on the edge of the shelf, it is slightly shifted to the north, and on the continental slope, this shelf is significantly stronger, at least to 26° N or even farther. Thus, the wider the bathymetric range of a species, the farther to the north boundary of its distribution extends.

The Fauna of Shrimp of Waters of Southwest Africa

This area extends from 17° to 34° S, and 24 species of shrimp belonging to the bottom–demersal complex were collected + here (Burukovskii and Romenskii, 1985, 1989) (Table 3), which is by one-third less than the species list of the adjacent region of the West African tropical region from Gabon to Angola (Burukovskii, 1978). Thus, the impoverishment of the shrimp fauna is observed in this case as well, resulting from both the absence of some species and lower frequencies of the remaining species. While north of 12° S, these frequences reach 100% everywhere (Burukovskii, 1978), in this region, they decrease to an average if 40%. The frequency of shrimp greatly varies by depths, especially in the lower part of the shelf, at its edge, and in the very upper part of the continental slope (boundaries between them are indicated by Burukovskii, 1984). Simultaneously, it changes along isobaths from north to south. Only at depths greater than 500 m does it reach 100%. In the northern part of this region, the shrimp occur at all depths, but on shallow areas, their frequency does not exceed 20%. In the middle zone (22°–28° S), at depths less than 200 m, shrimp are com-

pletely absent from trawl catches and occur again deeper than 200 m (frequency about 5%); south of 28° S, they occur again only in waters deeper than 300 m. On the outer shelf, a "shrimpless zone" is formed, shaped as a trapezium delimited by parallels 22° and 28° S, whose shoreward side coincides with the 100-m isobath and the seaward side, with the 200-m isobath in the north and 300-m isobath in the south (Burukovskii and Romenskii, 1985).

Shrimp found in this area belong to three faunistic groups. The first group lives in the northern part (16°–22° S) and comprises, *inter alia*, four endemic species of the West African zoogeographic region. This area is a southern periphery of the region. The second group lives in the middle part of the region (22°–28° S). Only six species are found there, two of which are endemics of the West African tropical province and one species of the South African province of the Indo–West Pacific region. This obviously is a transitional zone. The third faunal group lives to the south from 28° S and belongs to the South African province.

As in waters of West Sahara, some species form monospecific taxocenoses here. In the northern part of this region, this is *Plesionika acanthonotus*, and in the southern part *Merhippolite agulhasensis*. The former species from Morocco to Southern Angola occurs as single individuals and always with other shrimp species; from 17° S southward, *P. acanthonotus* is usually a sole species in catches and occurs as hundreds and sometimes thousands specimens.

DISCUSSION

Biogeographic analysis was only performed for shrimp of the bottom-demersal complex, and included none of the 65 holopelagic species that have no contact with the bottom. The island shrimp fauna (the Canary Islands, Cape Verde Islands, Pagalu, Sao Tome, and Principe) and shrimp from underwater elevations near African coast (Walvis Ridge), 24 species altogether, also remained beyond the scope of this study. The remaining 161 species are distributed along the West African coast very irregularly. The tropical fauna is the richest: 117 species (69.2%). The fauna of the Mauritania province is represented by 71 species (42.0%). The fauna of waters off Southwest Africa is the poorest: 28 species (16.6%).

In each region, the shrimp fauna is mixed and comprises the species in common with neighbors. Thus, in the Mauritania province of the Mediterranean–Lousitanian region, 38 species are common with the West African tropical region (49.3% of the species composition of the former and 32%—of the latter). The Jaccard's coefficient of similarity (Jaccard, 1908 cited after Valentine, 1966) between them is 25.3. With the shrimp fauna of the South African province, the Mauritania province has in common only 11 species and the West African tropical region 14 species; the coefficients of similarity between them are 12.5 and 10.7, respectively.

While a relatively high level of similarity of faunas of the Mediterranean–Lousitanian and the West African tropical regions depends on the presence of rather numerous species living only in these two regions, their similarity with the shrimp fauna of southern Africa is the result of widely distributed species that are Indo–Pacific in origin.

The main features of this pattern were already outlined by Crosnier and Forest (1973) with reference to the distribution of 32 species of bottom and demersal deep-water shrimp. The presence of numerous common species in the tropical zone and the northeastern areas of the Atlantic Ocean was explained by the system of currents distributing many species from the edge of the shelf up to the equatorial zone.

Indeed, the West African waters are characterized by a typical system of currents along the western coasts of continents, which may be termed a "locking system." These are two strong currents, the Canary Current and the Benguela Current (Vasil'ev and Makarevich, 1975; Shannon, 1972), preventing drift from the tropical zone and bringing into it representatives of the fauna of the adjacent regions from the north and south (Ekman, 1953; Manning, 1977). Such a current pattern explains the relatively high similarity, mainly due to species of the edge of the shelf, between the faunas of the Mauritania province and the West African tropical region. The same might be expected for the similarity level between the latter and the South African province of the Indo–West Pacific region. However, this is not observed in reality, implying the presence of a certain barrier between them (see below).

According to published data, the most characteristic trait of the boundaries is their diffuseness. Ekman (1935) and Balss (1957) noted that the northern boundary of the tropical region is situated near the Cape Verde (15° N), and the southern boundary near Angola (between 15 and 17° S). According to Nesis (1982), the boundary of the Mauritanian province is Cape Blanc (21°30′ N) or Cape Verde (15° N). The fact is overlooked that the southern and northern boundaries of areas inhabited by endemics of the tropical region and the southern boundaries of West Atlantic species ranges are removed from these points all the further the deeper these species live (Burukovskii, 1982; Burukovskii and Romenskii, 1985).

Thus, the northern boundary of the range of *Parapenaeopsis atlantica*, which lives at depths ranging from the water surface to 20–30 m, is situated at about 16° N (Burukovskii and Romenskii, 1995); of *Penaeus notialis* (15–50 m); Cape Blanc, 21° N (Burukovskii, 1982); and of *Plesionika carinata* (from 500–600 to 1000 m) at 26° N (Crosier and Forest, 1973; Burukovskii, 1982). The same is true of the southern boundaries of areas inhabited by these and other species (Burukovskii and Romenskii, 1985).

Thus, the boundary between two zoogeographic regions is located in the sublittoral zone (from 0 to 20–30 m) in the areas of 15°–16° N and 12°–13° S. On the open shelf, it is shifted to 21° N and 17° S, respectively. In case of species living on the shelf edge and continental slope, the northern boundary is situated at 26° N; the southern boundary at the edge of the shelf lies at about 22° S; and on the slope, at 26° S. It may be assumed that *the common trait of tropical zoogeographic regions of bottom–living organisms found off the western coasts of continents is their widening at greater depths*. Farther from the coast, they "wedge in" under the adjacent temperate zoogeographic regions, while the latter overlay the tropical regions and become narrower at greater depths. This phenomenon may be termed *the equatofugal subsurface shift in the boundaries of zoogeographical regions* (the term is derived from the words the equator and Latin *fugio*, to run, similarly to the term *centrifugal*). It should manifest itself in the zone extending to the continental slope where differences in physicogeographical characteristics of waters become significantly smaller (Neuman *et al.*, 1977). This is confirmed by a decrease in the proportion of endemics at greater depths and an increase in that of widely distributed species in shrimp taxocenoses at these depths, a kind of "erosion" of traits characteristic for this geographic region (Burukovskii, 1981).

The complexity of the spatial structure of the zoogeographic boundary does not contradict the fact that, in every depth zone, it tends to coincide with a certain complex of abiotic factors. Ekman (1935) connected them with specific isotherms. Today, it is generally accepted that the entire biogeographical structure of the ocean has a biotopical basis, namely the hydrologic structure (Beklemishev, 1969; Semenov, 1977). In West African waters, the boundary of shelf species clearly coincides with position of intertropical frontal zones in summer (Berrit, 1973): at Cape Blanc in the north and at Cape Frio in the south, 21° N and 15° S.

The distribution of shelf shrimp in boundary regions has certain pecularities apparently characteristic priliminary of these organisms, namely, the presence on the shelf of areas with impoverished species composition, low frequency in catches (up to complete absence), domination in remaining taxocenoses of species not dominant in adjacent areas (e.g., *Plesionika heterocarpus* off Western Sahara and *P. acanthonotus* off Southwest Africa), and disappearance of endemics. Thus, such areas lose characteristic zoogeographical traits. They have obvious traits of "the zone of impoverishment–transition" (Darlington, 1966) and differ from ecotones formed *inter alia* in the same areas at the shelf edge. The ecotone (the community limited in space and transitional between two neighboring clearly differing communities (Pianka, 1981) is characterized by overlaying of two neighboring communities and, hence, by mutual enrichment of fauna. In the present case, *the taxocenoses of shrimp are separated by a wedged-ingroup having its original traits, first of all, impoverishment*. Such areas may be designated *antiecotones*.

These boundary subregions also have their biotopical basis, as demonstrated by their symmetrical situation in relation to the equator (22°–28° N and S, respectively). Both ecotones are confined to the arid zone with active trade winds and arid type of mobilization and transfer of terrigenous material, on the one hand, and a high level of biological productivity resulting in humic sediments, on the other (Lushin *et al.*, 1967; Senin, 1974; Emel'yanov *et al.*, 1975). Bottom-living and demersal shrimp are usually the links of the detritus food chain (Burukovskii *et al.*, 1982; Burukovskii 1989a). Shelf shrimp are fully provided with autochthonous detritus (Beklemishev, 1976), and the absence of terrigenous sedimentation is of secondary importance. The "shrimpless" zones differ from other great trade wind areas with arid climate in the annual upwelling dynamics. The intensity of upwelling increases in summer, but not in winter (Sorkina, 1974; Furnestin, 1959; Allain, 1968; Shannon, 1972; Wooster *et al.*, 1976); as a result, some areas on the shelf of geographically subtropical regions have a water temperature in bottom layers that is more characteristic of the boreal and notal zones. This reduces the potential for the formation of shrimp fauna, as the regions inhabited by shrimp capable of living at such a temperature are separated by distances that the shrimp cannot over. In the southern region, the situation is complicated by the existence of a vast zone of grounds containing hydrogen sulfide, extending to 27° S. Its center is situated at depths of 70–160 m (Bulatov *et al.*, 1977), where there are no shrimp.

Such a strong barrier explains the great difference between the faunas of West African tropical region and the South African province of the Indo–Pacific region, which significantly exceeds the difference between the tropical and the Mauritanian provinces. The southern shrimpless zone is delimited by the depth of 500 m and the northern by the depth of 300 m. As a result, species of the shelf edge that form the shrimp fauna with interregional range type cannot penetrate from South Africa to the tropical zone.

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