

On the Role of Dense Aggregations of Males and Juveniles in the Functional Structure of the Range of the Blue Shark *Prionace glauca*

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Abstract—Analysis of the quantitative distribution and size composition indicated a high extent of the differentiation of the range of the blue shark *Prionace glauca*. This most abundant and widely distributed species in the oceanic epipelagial of the entire World Ocean remains for the first years of its life in coastal and neritic waters at depths of 80 m. At the earliest age, at a length under 70 cm, sexes separate into individual schools; females stay nearer to the coast. In the eastern Atlantic, two regions of juvenile habitats are recorded: to the north and to the south of the equator, with a typical gap between them in tropical waters. On reaching a length of 160–190 cm, sharks leave for oceanic waters; immature females follow dense aggregations of adult males situated in oceanic waters where their first mating takes place with a delayed fertilization until reaching sexual maturity. A similar pattern of distribution is traced in the eastern Pacific and other regions of the World Ocean. Under conditions of an increased demand and high prices of shark fins, such aggregations of juveniles and adult males where density exceeds average values dozens of times, can easily lead to overfishing and endanger the species existence and the stability of the structure of the oceanic biota as a whole. The necessity of introducing international protection measures with respect to such aggregations is substantiated.

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Having occupied a dominant position in the taxocenosis of Elastobranchii in the oceanic epipelagial in the recent geologic past, the blue shark *Prionace glauca* is currently the most widely distributed and one of the most abundant species (Compagno, 1984; Litvinov, 1989, 1997, 1998; Litvinov, 2004). Mejuto and García-Cortés (2004), based on data on catches per fishing effort, assume that *P. glauca* in the oceanic pelagial exceeds in abundance all large pelagic fish, both cartilaginous and bony, including tunas and Xiphiidae; that is, *P. glauca* namely, as the most abundant and widely distributed consument of a higher level, is a key species of pelagic ecosystems in temperate and tropical waters of the World Ocean.

Despite an increasing number of publications on Elasmobranchii, in general, and on *P. glauca*, in particular, much in the life cycle of this species remains poorly studied. The point is that the studies of recent years are based on materials collected mainly in fishery regions or in national waters (Hazin et al., 1990; Matsunaga and Nakano, 2000; Macias and Serna, 2002; Sosa-Nishizaki et al., 2002). Studies in remote oceanic waters are not adequately developed because they require large resources and are complex. A large pool of such data was obtained in the past by the Soviet fishery and research vessels: the USSR performed dozens of far expeditions to the open waters of the World Ocean in the 1960–1980s. Many applied and fundamental

issues related to the species composition and ecology of oceanic fish were studied (Parin et al., 1997; Nesterov, 2002). The data on the distribution of oceanic sharks in different sites of the Atlantic Ocean and the eastern part of the Pacific Ocean collected in expeditions of AtlantNIRO in 1978–1984 were generalized by the author (Litvinov, 1989). In particular, an important fact such as the formation by *P. glauca* of aggregations of a very high density in oceanic waters, often over seamounts, was recorded. Despite new detailed studies of the distribution, reproductive biology, and abundance of *P. glauca* performed in the framework of the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Mejuto and García-Cortés, 2004) and data based on a large body of material, the issue of the functional role of such aggregations has not been specially studied, although male dominance at the highest catches per fishing effort related to mating was recorded. The report on the world catch of *P. glauca* in the Atlantic (Anon., 2004) prepared for ICCAT does not cite data on the fishing of such aggregations. Apparently, this absence is related to the fact that the data on an by-catch of *P. glauca* in fishing of the tuna and Xiphiidae, rather than the data on a specialized fishery, were analyzed. There are still no official data on such fishery, but, according to data on the sale of meat and fins of *P. glauca* at world fish markets provided by FIS

Table 1. Dates and sites of material collection

No.	Year and month of catch	Number of sets (drifts)	Number of hooks at layers	Fishing gear	Number of caught blue sharks	Region, vessel
1	July–August 1978	15	12995	Bottom long-line	10	Coastal waters of northwestern Africa (28°46′–32°15′ N); ? 8002 <i>Vyandra</i>
2	November 1978	7	2100	Pelagic long-line	90	A complex of seamounts to the south of the Azores: Great Meteor, Hyére, Irving, Plato, Flamingo, Atlantis; medium refrigerated side-trawler 1257 <i>Langust</i>
3	November–January 1979–1980	14	2000	"	38	Coastal waters of northwestern Africa (29°42′–35°37′ N); medium refrigerated side-trawler 1257 <i>Langust</i>
4	September 1980	14	6045	Pelagic long-line	223	Northeastern part of the Walvis Ridge; medium refrigerated side-trawler 8018 <i>Kvant</i>
5	December 1980	5	1200	"	60	A complex of seamounts to the south of the Azores; medium refrigerated side-trawler 8018 <i>Kvant</i>
6	January–February 1981	12	3000	"	3	Coastal waters of Sierra Leone; medium refrigerated side-trawler 8018 <i>Kvant</i>
7	February–March 1981	5	1200	"	2	Coastal waters of Guinea-Bissau; medium refrigerated side-trawler 808 <i>Kvant</i>
8	June–September 1982	57	16806	"	176	Coastal and oceanic waters around the islands San Tome and Principe; medium refrigerated side-trawler 8030 <i>Spektr</i>
9	April–June 1984	37	5307	"	51	Eastern part of the Pacific Ocean, out at sea off Peru; medium refrigerated side-trawler 0815 <i>Blesk</i>
10	June 1984	4	1940	"	102	Eastern part of the Pacific Ocean, to the west of Galapagos; medium refrigerated side-trawler 0815 <i>Blesk</i>
11	April–June 1984	3	665	"	82	Eastern part of the Pacific Ocean, to the east of Galapagos; medium refrigerated side-trawler 0815 <i>Blesk</i>
12	July 1984	6		Pelagic and bottom trawls	7	Coastal waters of northeastern Africa (22°49′–23°31′ N); medium refrigerated trawler <i>Atlantida</i>
13	April 1987	2	105	Pelagic long-line	15	Eastern part of the Pacific Ocean, seamounts Nazca and Sala y Gomez; R/V <i>Professor Shtokman</i>
14	September 1992	1		Purse net	1	Pacific waters off Mexico, Ensenada; purse seiner <i>Lupe Del Mar</i>

(Fishery Information and Service, 2006), it has already been started.

In the light of the aforementioned, this paper concerns a detailed description and analysis of all our data and published data on the aggregations of *P. glauca* to determine their functional role in the structure of the range and to substantiate the necessity of species preservation under conditions of drastically increased fishery pressure.

MATERIAL AND METHODS

The material was collected by the author (except nos. 1, 5, and 6 in Table 1) in the period of 1978 to 1992

in the Atlantic Ocean and the eastern part of the Pacific Ocean. Studies were performed following the methodical recommendations of Ovchinnikov et al. (1985). Most of the material was collected using a pelagic tuna-longline; a minor portion of the material—by bottom longline, purse net, and pelagic and bottom trawls. The biological analysis included the measurement of total length (TL, the length from the snout tip to the end of the caudal lobe extended along the body axis) and the length to the caudal fork (FL) with an accuracy to 1 cm, the determination of the sex, stomach content, and other parameters.

For the assessment of the species abundance, we used the index of relative density (IRD) calculated as

the number of individuals of this species caught per 100 hooks of the pelagic long-line. IRD was calculated for individual drifts. For the determination of the total IRD of a particular species in local and extended sites, the ratio of the total number of caught individuals to the total number of hooks in all drifts was calculated. Therefore, the standard deviation (*SD*) of this parameter was not calculated.

IRD is a characteristic of the species abundance, and, during its calculation, parameters such as the vessel's crew skill or the quality of the used long-line were reduced to a minimum; i.e., all sharks caught by a hook were considered, including those that were not taken aboard for various reasons. The species, sex, and the size of these individuals were determined with a sufficient accuracy in most cases.

RESULTS AND DISCUSSION

The eastern Atlantic to the north of the equator.

As was demonstrated previously (Litvinov, 1989; 2004), *P. glauca* is unevenly distributed in the ocean: if for the open waters of the Atlantic and the eastern Pacific its IRD averages about 1.0, at particular sites, this value can be 10–20 times higher. Such sites were first revealed in November 1978 over the seamounts Meteor, Hyères, Irving, Plato, Flamingo, and Atlantis (south of the Azores). These data were confirmed in December 1980: the IRD calculated on the whole for the entire site of the seamounts comprised 9.81; it reached 14.0–22.3 at particular drifts over the seamounts. Such a density of sharks was observed at setting a pelagic long-line directly over the summits of seamounts and did not extend to adjacent waters. For instance, at setting a long-line between the seamounts Hyère and Irving, IRV comprised 0.67 (December 1980), and only 60 miles south of the Meteor Seamount, it was 0.33 (November 1978); i.e., in both cases it was lower than the average oceanic value.

In November 1978, 90 blue sharks, exclusively males with a length of 230–310 cm, were caught over the summits of seamounts. In December 1980, 60 blue sharks TL 170–310 cm, including only two females were caught. Males with a length of 230–280 cm accounted for 75% of the total number of the caught sharks (Figs. 1a, 1b). Thus, dense aggregations of males of a similar size composition were observed in the same region during two years, which implies their quasi-stationary pattern. Here and below, the aggregations of large males will be designated by the abbreviation MC ("male clubs").

The separate habitation of the sexes was recorded for *P. glauca* and other species of Elasmobranchii (Compagno, 1984). This phenomenon is generally related to the separation of food niches between the sexes. Since male sharks use teeth in mating, the teeth in males and females differ in the shape, which leads to differences in the feeding behavior and, finally, to a sep-

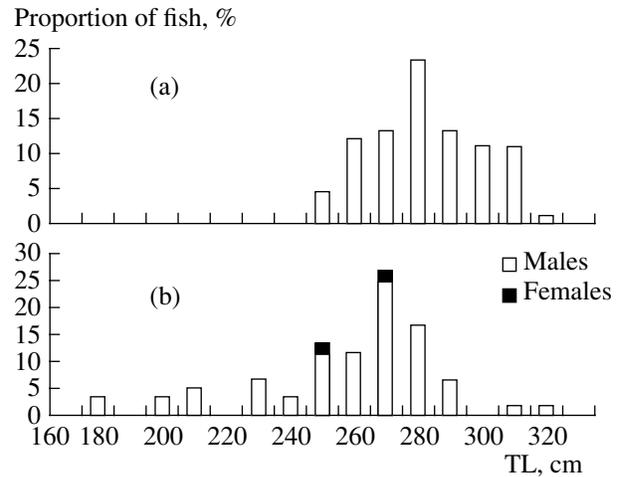


Fig. 1. Size and sex composition of the blue shark *Prionace glauca* in catches at seamounts of the southern Azores complex: (a) November 1978; (b) December 1980.

arate habitation (Litvinov, 2003; Patokina and Litvinov, 2004; Litvinov and Laptikhovskiy, 2005). This explanation is obviously insufficient for the MC phenomenon, since we deal with quasi-stationary aggregations of an increased density consisting exclusively of adult males and attributed to the summits of seamounts as to a certain landmark, rather than with groups of males and females that stay in isolation but inhabit the same regions (which will be described in more detail for the Walvis Ridge). In the animal world, such aggregations are well known for mammals and birds; their main aim is to facilitate the meeting of the partners and, hence, subsequent mating.

This viewpoint is supported by the presence of the aggregation of juvenile *P. glauca* east of the MC described in coastal waters of northwestern Africa at a latitude of 35°30'–22°49' N. The sites of setting fishing gear in this region are indicated in Fig. 2. In November 1979–January 1980, 38 blue sharks were caught at depths of 260–1200 m at a distance of 25–35 miles from the coast at 14 settings of a pelagic long-line in coastal waters of northwestern Africa. The bulk of the catch consisted of juvenile sharks with a length of 90–160 cm. In the range of sizes 130–160 cm, the sex ratio was nearly equal; females dominated among smaller sharks (Fig. 3). In addition, in July–August 1978, ten blue sharks with a length of 121–150 cm (two males and eight females) were caught in the bottom long-line in the same region at a depth of 62–80 m at a distance of 15–20 miles from the coast (Fig. 2). On the whole, juvenile females stay nearer to the coast than juvenile males. In July 1984, seven blue sharks with a length of 70–116 cm (four males and three females) were caught with pelagic and bottom trawls further to the south (22°49'–23°30' N) over depths of 93–610 m. These were "kindergartens" (KG) of *P. glauca*, according to our data, which extend in the northern hemisphere, as a minimum, from Gibraltar to 22°49' N.

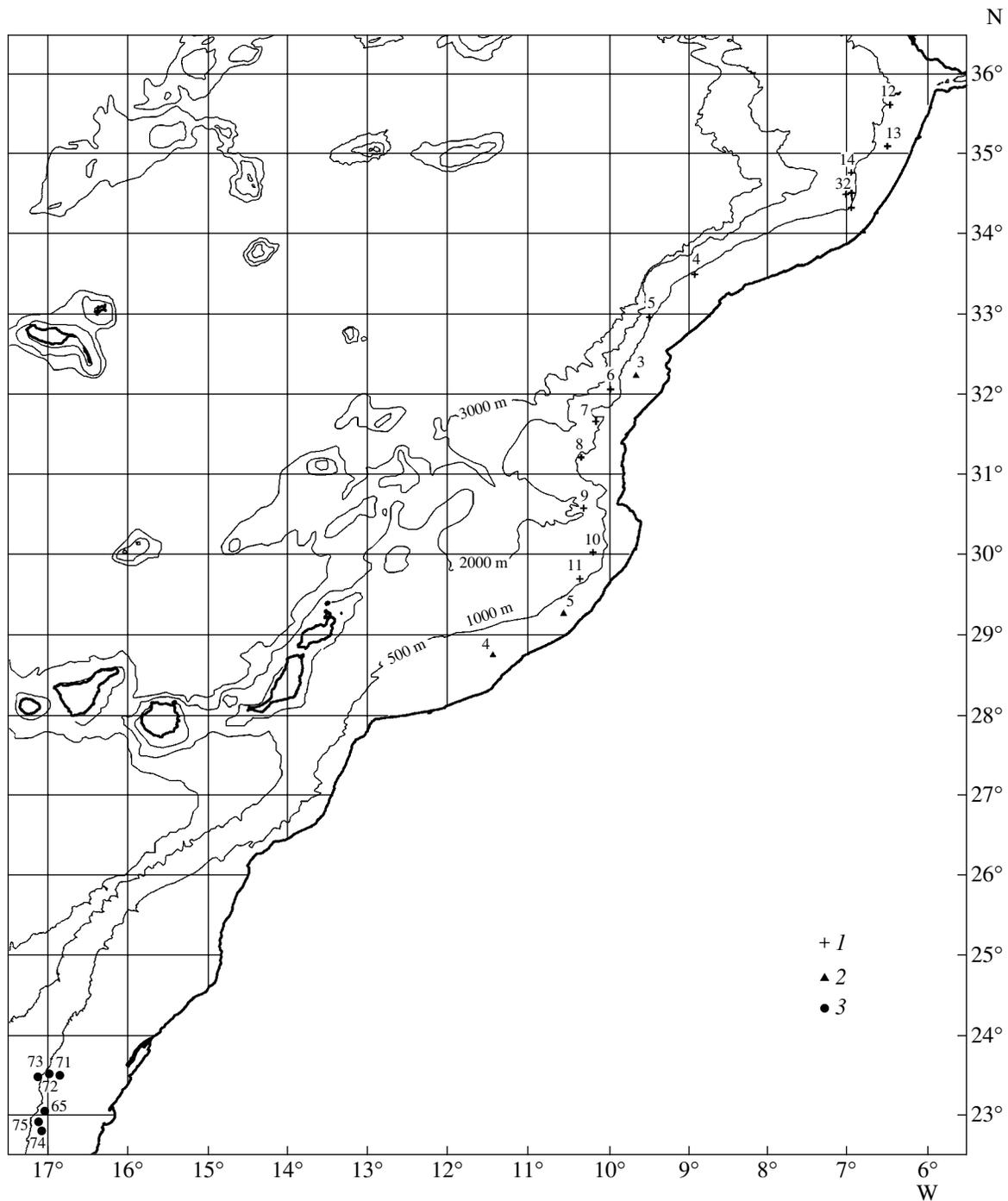


Fig. 2. The distribution of catches of the blue shark *Prionace glauca* in waters of northwestern Africa: (1) pelagic long-line, November 1979–January 1980; (2) bottom long-line, July–August 1978; (3) pelagic and bottom trawls, July 1984.

P. glauca is among the most oceanic shark species (Compagno, 1984; Litvinov, 1989, 2004). However, considering the presence of juvenile aggregations in the coastal zone at depths of 62 m, this species, according to the classification of Parin (1968), should be assigned to epheboepipelagic species dwelling in the upper long-lines of the oceanic pelagial in an adult state, but reproducing in coastal marine waters, rather than to holoepi-

pelagic species. The habitation of juveniles in coastal waters, including mangrove vegetation, is known for several species of neritic sharks: *Carcharhinus albimarginatus*, *C. altimus*, *C. obscurus*, etc. (Compagno, 1984).

In all probability, immature females aged four to five years leave KG and migrate to MC for the first copulation. Then the sperm is retained in shell glands for a

long time until the maturation of the first batch of eggs and fertilization (Pratt, 1979; Compagno, 1984). This portion of sperm is also used for the subsequent series of repeated insemination (Pratt, 1993). Therefore, in the reproductive strategy of the species, the first copulation is very important in terms of energy saving since it takes place near the sites of juvenile concentration and does not require far migrations to the sites of copulation, for, at least, several years. In this case, the summits of seamounts serve as landmarks facilitating the meeting of partners. Thus, in the eastern Atlantic north of the equator, a pair of closely situated aggregations of *P. glauca* was recorded: MC consisting of adult males and KG within which juveniles stay until leaving for oceanic waters.

The eastern Atlantic south of the equator. In September 1980, 223 individuals of *P. glauca* TL 60 to 290 were caught in the area of seamounts of the Walvis Ridge (Fig. 4). In the combined histogram of the size and sex composition, a minimum of three size groups are distinctly discerned: 60–110, 120–200, and 230–290 cm (Fig. 5o). The range of sizes of 120–200 cm includes not less than three size groups, although the boundaries between them are pronounced less distinctly. The total sex ratio at the site on the whole and in most size groups was about 1 : 1; only among sharks longer than 240 cm were males were dominant. It is interesting to note that the sex ratio considerably varied at particular drifts of the pelagic long-line in this zone; a catch could consist almost exclusively of representatives of one sex and of different sizes. Thus, in two long-lines set at a depth under 1000 m at a distance of 50–55 miles from the coast, the sex ratio was 4 : 45 and 2 : 11 (Figs. 5m, 5n), while at the site out at sea, at a distance of 200–300 miles from the coast, males prevailed, both juveniles and adults (Figs. 5c, 5d). The distribution of juveniles exhibits the same regularity as in the northern hemisphere: males and females stay in a neritic zone, but female aggregations are situated closer to the coast.

Sex segregation takes place rather early—at a length of sharks under 70 cm. Dense aggregations were formed by females in the coastal part of the site (IRD = 12.3; Fig. 5m) and by males at the site out at sea (IRD = 6.1; Fig. 5d). In this case, the presence of KG is clearly traced; the proportion of large males with a length over 240 cm increases with distance from the coast, but there are no distinctly pronounced MC as yet here. Most likely, they are situated at a larger distance from the coast as in the northern hemisphere.

Thus, one can note the presence of a clearly pronounced pair of aggregations (MC in oceanic waters and KG in coastal waters) in the eastern Atlantic in the northern hemisphere. This pair has an analog in the southern hemisphere where KG are well pronounced, and the presence of MC is expressed in an increase of adult males in the part of the site out at sea. There is a discontinuity between KG of *P. glauca* in the north and

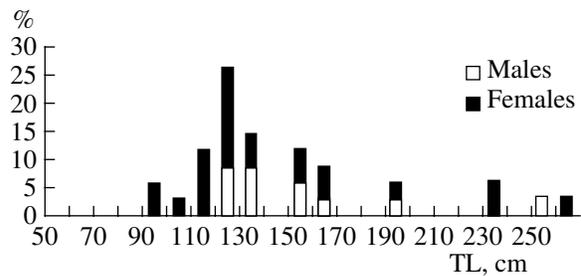


Fig. 3. Size and sex composition of the blue shark *Prionace glauca* in November 1979–January 1980 in coastal waters of northwestern Africa (29°42'–35°37' N).

south of the eastern Atlantic: according to the data of surveys performed by a pelagic long-line in waters of Sierra Leone in January–February and Guinea-Bissau in March 1980; *P. glauca* was represented only by adult females caught beyond the edge of the shelf. Both juvenile and adult sharks were lacking in the shelf waters; the water temperature here is too high for *P. glauca*, and it is replaced by *Carcharhinus falciformis* (Litvinov, 1989).

Equatorial oceanic waters of the eastern Atlantic. According to the data of Castro and Mejuto (1995), most females of *P. glauca* caught in June–August 1993 in the Gulf of Guinea contained embryos. Based on the maximum sizes of embryos, a suggestion was made that females migrate from west to east to the spawning grounds along the equator in the eastern Atlantic. In fact, if juvenile *P. glauca* cannot live on the shelf of the tropical and equatorial zone because of the vertical warming of shelf waters (according to the data of telemetric observations, the temperature optimum was within 14–16°C (Sciarotta and Nelson, 1977), one can suggest its presence near islands or seamounts where there is a distinct vertical stratigraphy of waters. According to our data, in the oceanic part of the Gulf of Guinea, in waters of São Tome and Principe, two zones, a 30-mile zone off the island and an oceanic zone situated 30 to 200 miles from the coast, are distinguished by the species composition and the extent of domination. In both zones, *P. glauca* prevails; its total IRD in the oceanic zone is 1.91, and in the zone off the island, it declines to 0.68; here, as in tropical coastal waters, the relative value of IRD of the subdominant species, *C. falciformis*, drastically increases (Litvinov, 1989).

In the zone off the island, the sex ratio was in general equal, but among sharks longer than 240 cm, males were dominant (Fig. 6b). In the oceanic zone, sharks were larger—200 to 310 cm; the sex ratio was 3 : 1 (Fig. 6a). Of 49 females taken aboard, 37 (76%) were pregnant (in 36 females, uteruses contained embryos; in one female, eggs at the initial stage of development). The length of these females varied from 185 to 305 cm and the sizes of embryos, from 5 to 41 cm; their number was 5 to 60. Of 12 nonpregnant females, 11 (92%) had fresh bites on the back, sides, and in the region of the anus—typical traces of recent copulation. Only one

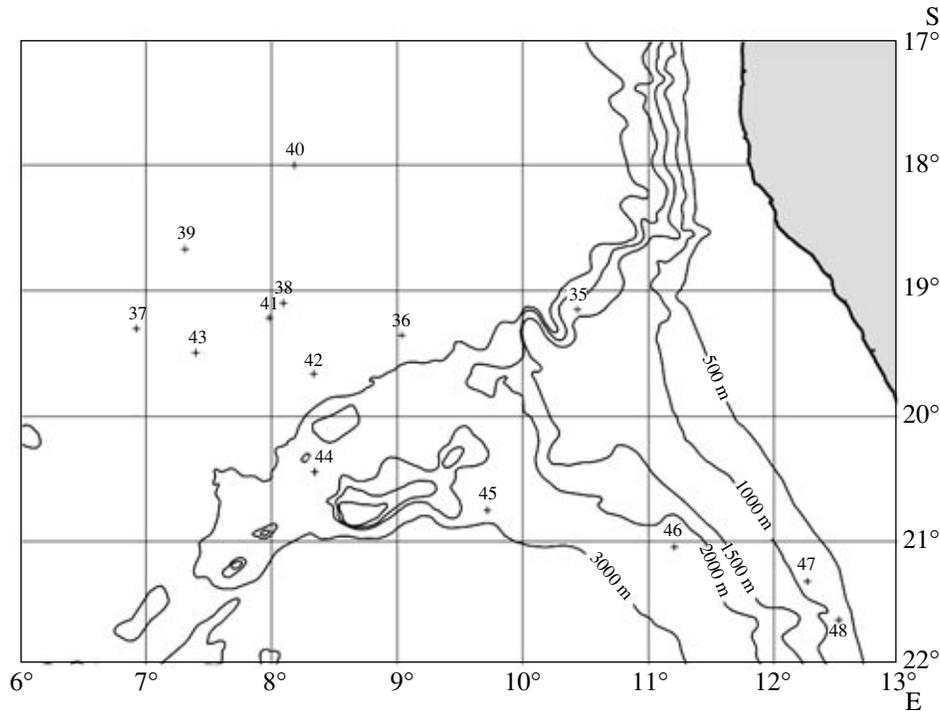


Fig. 4. The location of long-line catches in September 1980 in the area of the northeastern part of the Walvis Ridge. Abundance of long-lines are designated by figures.

nonpregnant female (TL 242 cm) had no bites; while among pregnant females, only one that contained 28 embryos with a size of 12–16 cm had typical copulative bites. Thus, in waters of São Tomé and Príncipe, there is a typical MC similar in size and age composition with male aggregations over the southern-Azores complex of seamounts. Judging from the sizes of females with fresh bites (TL 185–273 cm), here we deal with repeated copulations of females rather than with only (or not so much) first copulations of females. The period of staying of females ready for copulation in the MC zone is limited; they leave this place soon after the copulation. However, the presence of some number of pregnant females within MC is common in both the Atlantic and Pacific oceans. Most likely, from the first stages of pregnancy (not later than the emergence of eggs in the uteruses), mechanisms hindering the subsequent courtship on the part of males are triggered, and pregnant females can return to the MC zone. Although, as was demonstrated above, errors are possible in the mating behavior.

The total IRD is low here, it exceeds the average oceanic only two times, but at particular drifts, IRD reaches 4.6. No traces of the presence of KG in the tropical zone of the eastern Atlantic were found (either off the continent, or in zones off the island). Most likely, the females from the Gulf of Guinea at later stages of pregnancy migrate for spawning to the north and/or to the south to colder waters of both hemispheres rather than spawn in the vicinity of the equator. In the coastal

waters of the eastern Pacific, such a gap can be lacking due to the impact of cold waters of the Humboldt Current (see below).

The presence of two MC to the north and south of the equator suggests the respective existence of two stock units, possibly, of a subspecies rank. The suggestion concerning the existence of such units (Litvinov, 1989) was supported by the data of marking and the rates of growth (Casey and Kohler, 1991; Lessa et al., 2004) and is now considered universally adopted (Anon., 2004; Mejuto and García-Cortés, 2004).

P. glauca juveniles were also recorded in the northern Atlantic between 30–40° N. It is assumed that newborn females migrate to the north, and then, on reaching sexual maturity, to the south; newborn males migrate to the south and stay there upon reaching sexual maturity (Anon., 2004). According to our data, in the KG of the southern hemisphere, a sex ratio of about 1 : 1 is retained on the whole (Fig. 5); in the northern hemisphere, junior age groups (90–110 cm TL) are composed exclusively of females; in older groups, the sex ratio is leveled (Fig. 3). Apparently, in the northern hemisphere, a certain spatial redistribution of newborns occurs after spawning; females arrive earlier to the KG of northwestern Africa; but, on reaching a length over 110 cm, the sex ratio becomes equal, possibly, due to the cessation of migration. It remains unclear where in such a case spawning occurs. If it takes place near the equator, as Castro and Mejuto (1995) suppose, such distant migration of newborns does not seem energeti-

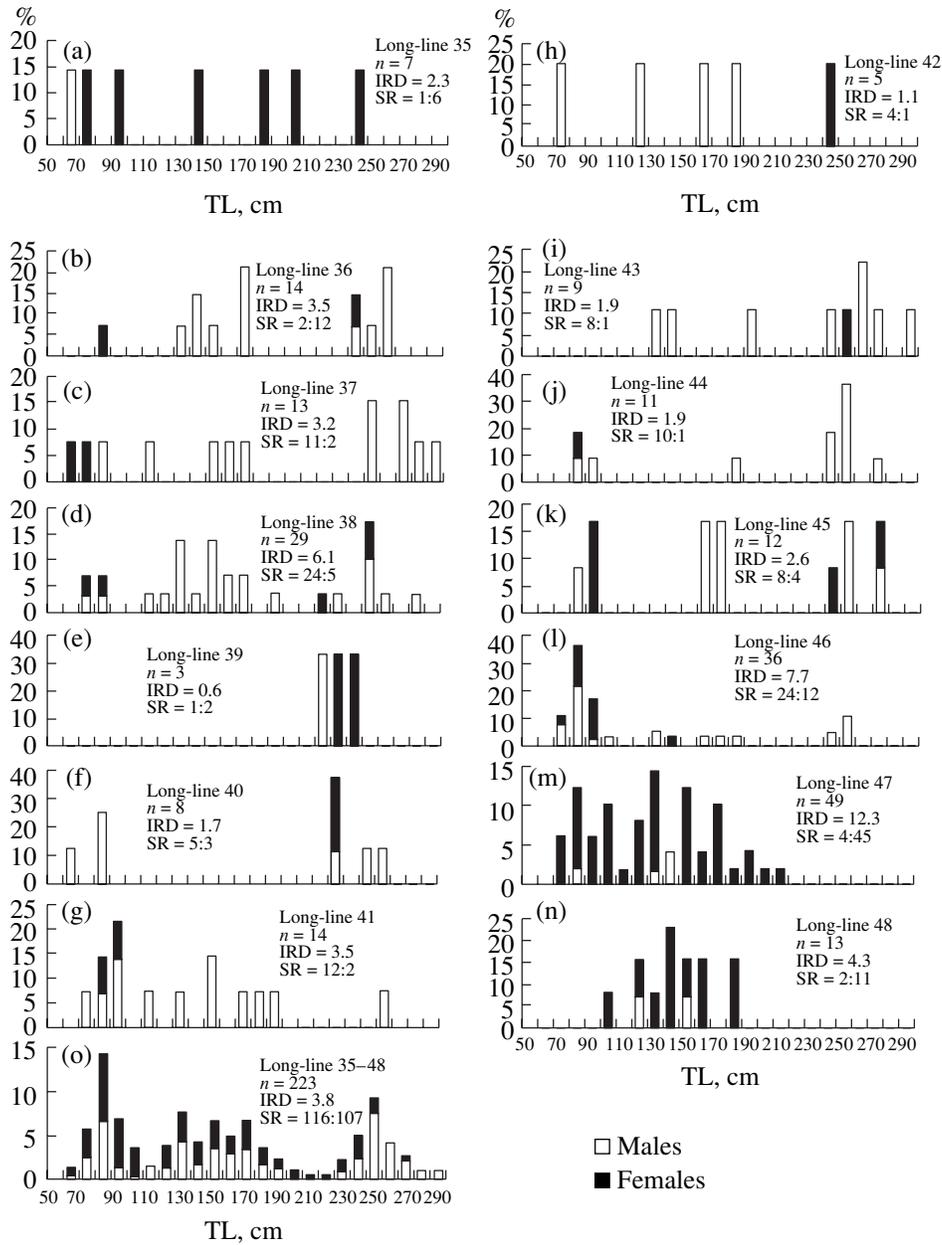


Fig. 5. Size and sex composition of the blue shark *Prionace glauca* in catches by pelagic tuna-catching long-line in September 1980 in the area of the northeastern part of the Walvis Ridge: (a–n) histograms for particular catches; (o) total histogram; *n*, number of blue sharks in a long-line; SR—the sex ratio—males : females. Numbering of long-lines is the same as in Fig. 4.

cally justified. More likely, the spawning grounds are situated in coastal waters of northwestern and southwestern Africa.

The eastern Pacific. Dense aggregations of *P. glauca* males were found in the eastern Pacific: east of (IRD = 12.9) and west (IRD = 5.9) the Galapagos Islands (Litvinov, 1989). The western aggregation consisted mainly of adult males TL 190–250 cm (79.4% of all sharks taken aboard) (Fig. 7a). Of 11 females taken aboard, nine (82%) were pregnant; in eight females, uteruses contained 19 to 54 embryos with a size of 5 to

41 cm; in one female (TL 210 cm), 27 eggs at the initial stage of development. The last female had old bites, traces of former copulation. Two nonpregnant females had no traces of copulation; their uteruses were strongly widened and filled up with water, possibly, due to recent spawning. The aggregation east of the island was very similar to the western aggregation (Fig. 7b); it consisted mainly of males with a length of 180–240 cm (80.5% of all sharks taken aboard). Of 13 females taken aboard, 12 were pregnant; they contained in the uteruses 13–48 embryos with a length of 17–41 cm each. In a single nonpregnant female, uteruses were filled up

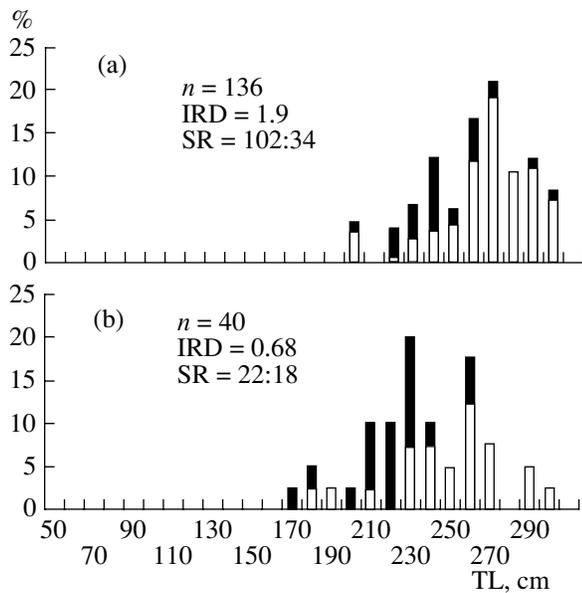


Fig. 6. Size and sex composition of the blue shark *Prionace glauca* in waters of São Tome and Principe in June–September 1982: (a) oceanic zone; (b) zone off the island. Abbreviations as in Fig. 5.

with water and swollen; it had no traces of copulation. Thus, both aggregations were typical MC close in the size and age composition to the aforementioned MC from the eastern Atlantic. It should be noted that in the MC of the eastern Pacific, males are, on the whole, smaller than in the eastern Atlantic where the dominant length is 240–300 cm, apparently, as a result of differences in the rate of growth of *P. glauca*.

South of these MC, beyond the economic zone of Peru, the total IRD of *P. glauca* was 1.2; i.e., it was close to the average oceanic value. Here, sharks with a length of 150 to 290 cm were caught (Fig. 7c); in the size groups over 200 cm, the sex ratio was nearly equal; among smaller sharks, males dominated. Most likely, juvenile males with a length of 150–190 cm dwelling here are a derivative of a KG situated in the coastal waters of Peru. As was shown above, smaller individuals and females stay closer to the coast. Of 14 females taken aboard, 12 contained in the uteruses 25–75 embryos with a length of 7–41 cm each. Two nonpregnant females with a length of 165 and 195 cm had no traces of copulation; their uteruses were not swollen and were not filled up with water. Apparently, these females were on the threshold or at the beginning of migration from a coastal KG to the nearest MC. It was not necessarily towards one situated off the Galapagos Islands: in April 1987, further to the south, over the summits of seamounts of Nazca Ridge, still another MC (IRD = 15.0) consisting exclusively of males with a length of 191–288 cm was found (Fig. 8).

According to published data, KG are widely represented in coastal waters of the eastern Pacific, including

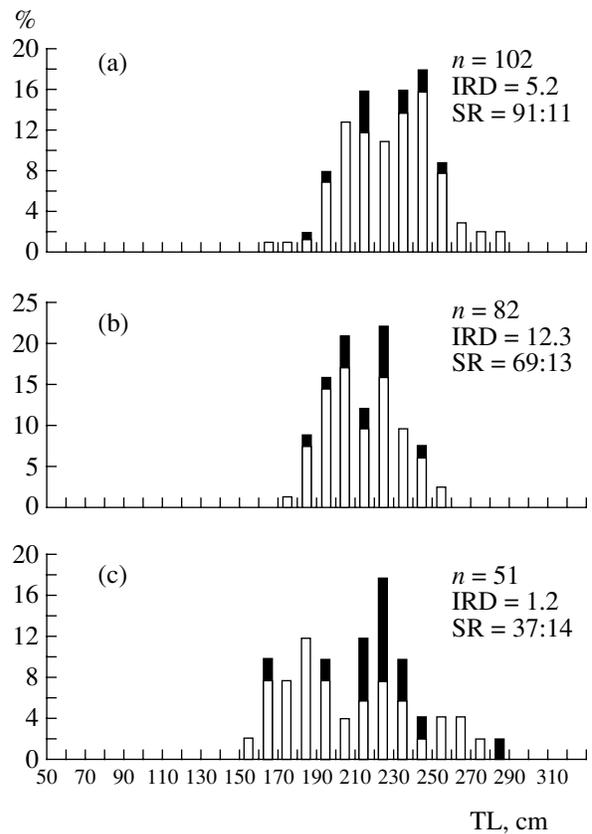


Fig. 7. Size and sex composition of the blue shark *Prionace glauca* in the eastern part of the Pacific Ocean in April–June 1984: (a) to the west; (b) to the east of the Galapagos Islands; (c) in open waters to the west of the exclusive economic zone of Peru. Abbreviations as in Fig. 5.

the tropical zone, due to the cooling impact of the Humboldt Current (Fig. 8). For instance, Brenes et al. (2000) note the presence of *P. glauca* juveniles with a length of 60 cm and over in Pacific waters of Nicaragua. Love (1991) states the presence of *P. glauca* juveniles with a length of 90–120 cm in the vicinity of Santa Barbara. South of the boundary between the United States and Mexico, a female *P. glauca* with a length of 86 cm was obtained by the author of this article in the course of the inspection control of purse seines of the Mexican tuna-catching fleet by the representatives of IATTC in September 1992.

According to the data of analysis of the coastal specialized fishery of *P. glauca* and by catch in swordfish fishery, the average length of *P. glauca* in coastal waters west of Baja California is 119 cm and in waters out at sea, 177 cm (Sosa-Nishizaki et al., 2002).

Thus, in the eastern Pacific, as in the eastern Atlantic, there are KG in coastal waters and MC located near in the oceanic waters.

KG can occupy rather extended areas: according to the data of Macnaughton et al. (1998), the modal length of *P. glauca* in the Atlantic in catches by gill nets

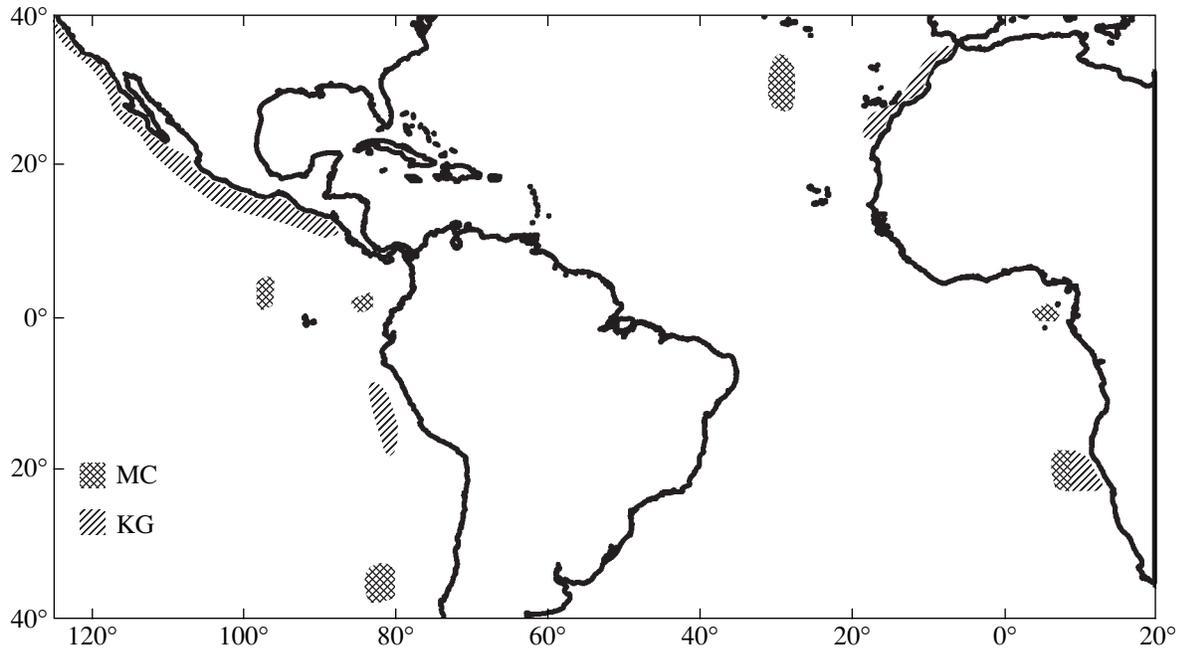


Fig. 8. The distribution of KG and MC of the blue shark *Prionace glauca* in the eastern Atlantic and the eastern Pacific (according to our and published data).

between 46 and 52° N is 120–130 cm at a total sex ratio of 1 : 1. Thus, there is either one large kindergarten or more likely a group of smaller KG. Casey and Kohler (1991) assume that one panmictic population of *P. glauca* exists in the northern Atlantic. Considering the aforementioned data on the presence of KG in the coastal waters of northwestern Africa and the data of Macnaughton et al. (1998), it can be assumed that in the Atlantic, north of the equator, there are, at least, two subpopulations: one spawns north of 46° N; the other, in West African and, apparently, West European coastal waters.

The distribution of KG and MC is not restricted to the waters of the eastern Atlantic and the eastern Pacific. According to the data of commercial statistics, such formations are present, for instance, in waters of Tasmania: KG consist mainly of females, which is related to the seasonal pattern of fishery (Stevens, 1992). According to the aforementioned data on the spatial position of the aggregation pairs, one can predict with assurance the existence of a MC either in the immediate vicinity of them in a site out at sea or at some distance—near pronounced landmarks (seamounts or quasi-stationary gradients of oceanic waters). Considering a wide distribution of *P. glauca* in the World Ocean, undoubtedly, future oriented studies will reveal a considerably higher number of pairs of KG and MC within its range than is provided in this article.

The ways of formation and the significance of KG and MC. In the distribution of *P. glauca* juveniles within KG, a pattern similar to that in the distribution of *Scyliorhinus canicula* is observed: males and

females stay separately from each other, but the distance between the groups is small, and they mix rather often (Litvinov, 2003). Because of the use of teeth by males during copulation, the teeth of males and females have morphological differences: teeth cusp in females are wider; their serration is rougher than in males. Such differences in *P. glauca* become more noticeable with growth, but are present in juveniles also (Litvinov and Laptikhovsky, 2005). Different dental form in males and females suggests differences in the feeding behavior, which apparently leads to an early spatial segregation of the sexes. With an increase in length, dental differences become more pronounced, and the subsequent spatial isolation of the sexes and the formation of MC occur. The stomachs of all seven sharks caught in July 1984 by pelagic and bottom trawls in waters of northwestern Africa contained food; in representatives of both sexes, these were exclusively pelagic organisms, but the food composition of males and females differed, as far as one can judge from this scanty material (Table 2).

Unfortunately, the stomach content of *P. glauca* caught by a pelagic long-line is not always suitable for analysis since, during sampling, a considerable part of stomachs is everted and rather frequently set back by the water flow. As a result, the stomach content is lost, and the stomach fullness index is designated as 0. For instance, during the work with a pelagic long-line in November 1979–January 1980, of 38 caught sharks, in all males and in 65% of females, stomachs were empty, everted, or contained only bait. In the food of females, cephalopods dominated (85% of full stomachs); two

Table 2. Food composition of blue sharks *Prionace glauca* caught by bottom and pelagic trawls in waters of northwestern Africa in July 1984

TL of blue sharks, cm	Food components		Type of the trawl	Depth, m
	object	proportion by weight, %		
Males				
93	<i>Trachurus</i> sp.	100	pelagic	275–210
63	Engraulidae	80	bottom	94–93
	Squid	20		
70	Engraulidae	100	pelagic	93
80	Engraulidae	100	"	93
Females				
95	<i>Scomber</i> sp.	71.4	"	275–230
	Myctophidae	28.6		
116	Myctophidae	99	"	610–600
	Euphausiidae	1		
97	<i>Trachurus</i> sp.	100	"	95–93

stomachs contained remnants of fish; and one stomach, birds.

Data on the feeding of *P. glauca* males and females are not separated in the literature (Compagno, 1984; Harvey, 1989). In the largest sharks that are most spatially isolated, teeth are obviously suited for different kinds of food (Litvinov and Laptikhovskiy, 2005). It can be assumed that males having finely serrulated narrow awl-shaped teeth are adapted to feeding mainly on small organisms that do not require cutting before swallowing; females with roughly serrated wide triangular teeth can fully feed on larger animals (corpses) also, including birds and mammals.

Under conditions of a "shark boom," the presence of local juvenile and male aggregations in the absence of a proper international control of fishery is a hazard for the species existence (Litvinov, 2004). If, until recently, the price of a ton of the frozen meat of *P. glauca* did not exceed \$1000–1200 for a ton on the world market, according to the last data of the Fish Information Service, this value has increased to 5700 EUR, i.e., almost five-fold. The price of a ton of frozen fins is 40 000–50 000 EUR. For comparison: the price of a ton of frozen meat of swordfish is 5400 EUR and of *Galeorhinus galeus*, 1800 EUR. According to the data of ICCAT (Anon., 2004), the fins of *P. glauca* during last years comprised up to 18% of the volume of trade in fins in the markets of Hong Kong, while the fins of *Isurus oxyrinchus* made up 2%. The specialized fishery intended to shark-fins exceeds in profitability today most species of oceanic fishery, and pelagic sharks can be exterminated much more rapidly than whales in the recent past. Moreover, *P. glauca* is much more sensitive to the impact of fishery in comparison with large tunas—objects of long-line fishery (Schindler et al., 2002). Besides overfishing, this typically oceanic species in

some regions is endangered by poisoning with chemical pollutants (Corsolini and Focardi, 2002). Some MC and KG are within the zones of national jurisdiction (coastal countries of western Africa and western coasts of both Americas; waters of São Tome and Príncipe) and are, as one would like to hope, a subject of concern on the part of national fishery legislations as a part of natural resources. But most MC are situated in open waters, and their protection needs combined international measures on the part of FAO and international fishery commissions (ICCAT, IATTC (Inter-American Tropical Tuna Commission), etc.).

The role of oceanic MC in the ecosystems of seamounts in the vicinity of which they exist remains not quite clear and underestimated. The impact of dense aggregations of large predators on the population of seamounts can be rather considerable. Since *P. glauca* due to its abundance and distribution is currently one of the key species of the oceanic ecosystem, a drastic decrease in its abundance as a result of the impact of fishery can cause a radical rearrangement of this ecosystem on the whole. As was shown previously (Litvinov, 1997, 1998), *P. glauca* in the recent geologic past has drastically increased its abundance and replaced sharks of the genus *Isurus* from the dominant positions. The causes of such replacement and its consequences for the oceanic ecosystems remain unknown up to the present time.

CONCLUSIONS

In the functional structure of the range of *P. glauca*, two types of spatially isolated formations of a quasi-stationary pattern, differing in the size and sex composition and the role in the life cycle, are distinguished. The species density in these formations exceeds aver-

age oceanic values five–twenty times. These are aggregations of large adult males (MC) and immature juveniles (KG). MC are situated in oceanic waters and are related to permanently existing large-scale landmarks: seamounts (seamounts of the southern-Azores complex, Walvis Ridge, Nazca Ridge), islands (São Tome and Principe), and zones with an active water dynamics (regions west and east of the Galapagos Islands). In the last case, a double orientation is likely used: at the islands themselves and at the drastically pronounced temperature gradients west and east of them caused by the impact of the Humboldt Current. In MC, adult males absolutely dominate: with a length of 240–300 cm in the eastern Atlantic and 200–270 cm in the eastern Pacific. The main purpose of MC is provision of mating. In males that reached such lengths, considerable changes in the dental form occur oriented at minimization of the female skin damage when retaining it during copulation. In turn, the thickness of skin in females increases several times. Mating has a seasonal pattern; females leave MC soon after copulation. Fertilization in adult females can occur soon after mating; in juvenile females, it is delayed for several years, up to egg maturation. Upon fertilization, at the initial stages of egg development in the uteruses, a readjustment of mechanisms controlling mating behavior occurs, and pregnant females can stay in the MC zone causing, as a rule, no courtship on the part of males. Females at different stages of pregnancy (from initial to final) can stay within the MC; the water area occupied by the MC is only a feeding ground for them. Females with completely formed embryos (with a length of 35–40 cm) migrate to neritic waters where spawning takes place. Newborn blue sharks migrate to the formations of the second type—KG that are situated in coastal and neritic waters (over depths of 62 m and larger, up to oceanic). At an early age, at a shark length of no more than 70 cm, sharks separate into individual schools consisting of representatives of one sex. On the whole, smaller sharks stay nearer to the coast than larger sharks, and female schools stay nearer to the coast than male schools. However, schools of juvenile males and females stay not far from each other. The cause of their spatial isolation at such an early age can in no way be related to the mating behavior; it is rather induced by differences in the feeding since differences in the form of teeth cusp in males and females are manifested at the earliest age. On reaching the length of 170–180 cm, females leave KG and migrate to MC where their first mating takes place. Then egg maturation and fertilization follow, and the aforementioned cycle is repeated.

The presence in the structure of the range of dense aggregations of a quasi-stationary pattern under conditions of a drastically increased pressure of fishery can endanger the existence of both *P. glauca* and the oceanic ecosystems of which it is a component.

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