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Translation

BEHAVIOR AND BIOACOUSTICS OF DOLPHINS

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BEHAVIOR AND BIOACOUSTICS OF DOLPHINS

Moscow POVEDENIYE I BIOAKUSTIKA DEL'FINOV in Russian 1978
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STRUCTURE OF A HERD OF BOTTLENOSE DOLPHINS

Moscow POVEDENIYE I BIOAKUSTIKA DEL'FINOV in Russian 1978 pp 9-33

[Article by V. M. Bel'kovich, A. V. Agafonov, O. V. Yefremenkova, L. V. Kozarovitskiy, S. P. Kharitonov]

[Text] There is still no precise information on the population structure of the Black Sea Afalina [*Tursiops truncatus* Montagu] bottlenose dolphins, and no one has data on the migrations of dolphins of this species, the size of the water areas occupied by them, the pulses of the areal, the numerical size of each of the populations of bottlenose dolphins, etc. One of the approaches to research on this question is a study of bottlenose dolphins in a certain region, which may serve as a convenient model and gives reason to hope that an acceptable solution to the problem will be found.

Bottlenose Dolphins (Afalina)

Using as a basis personal observations in the eastern Crimea and near the coastal area of the Caucasus, as well as data from an inquiry of fishermen, we took as a working hypothesis the fact that Black Sea bottlenose dolphins are settled animals, and their population is represented by local subpopulations. In this case we took as the local subpopulation the aggregate of bottlenose dolphins inhabiting this section of the water area.

To designate the structural subdivisions of the local subpopulation of bottlenose dolphins we used certain generally accepted terms: group, herd, school.

By herd we mean the natural grouping of dolphins characterized by the use of a certain water area, prolonged independent existence, unity of the vital activity and, obviously, the kinship of the animals among themselves. The term "group" we use to designate the elementary unit of the herd. Groups are the components of the herd and evidently do not exist for long when detached from the herd. The school is regarded as an unstable union of several herds.

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The structure of the population and any part of it may be characterized by the criteria of sex, age and spatial and behavioral differentiation (Naumov, 1964, 1972).

When observing the bottlenose dolphins we did not succeed in establishing the sexual composition of the herd, since the bottlenose dolphins have no sexual dimorphism as do, for example, *Orcinus orca* (Spong et al., 1970). If, however, the animal was swimming with the young dolphins, it could be assumed with great probability that this was a female, because observations in oceanariums show that most of the time the young dolphins go with the mother. In a sufficiently large number of observations it proved to be possible to fix the age structure of the herd according to the system: adults and young. The young dolphins less than one year old were very easily distinguished by size, being approximately 1/3-1/2 the length of the adult. As a rule, when in motion they kept somewhat behind and to the side of the female and would surface with her. Sometimes, in close passes, it was possible to distinguish the adolescents (subadultus) by size as well--3/4 the length of the body of the adult bottlenose dolphins.

Spatial and Behavioral Structure

When observing bottlenose dolphins in the sea we most often saw a group of animals or several groups. The animals in one group would usually remain closer to one another than the animals of different groups. Each group was characterized by greater unity of activity than the herd as a whole, made up of them.

Therefore, with the bottlenose dolphin we are dealing with a group structure of the herd, typical for many species of cetaceans (Yablokov, et al., 1972). Usually groups of two, three, four and five animals were observed, which was also noted earlier for other toothed whales--belugas (Bel'kovich, 1960). The group structure of the herd was easily distinguished during its movement in the water area. In this case various types of formation of the herd were observed, which received the following names: "chain," "front," "line," "direction-finding," "double front" and "double direction-finding" (Figure 1).

When moving as a front, the dolphins were often arranged uniformly, and the group structure seemingly disappeared. The group structure could not be seen, or only faintly traced with the reaction of fright, when the animals would gather under water and surface in a dense herd, far from the danger.

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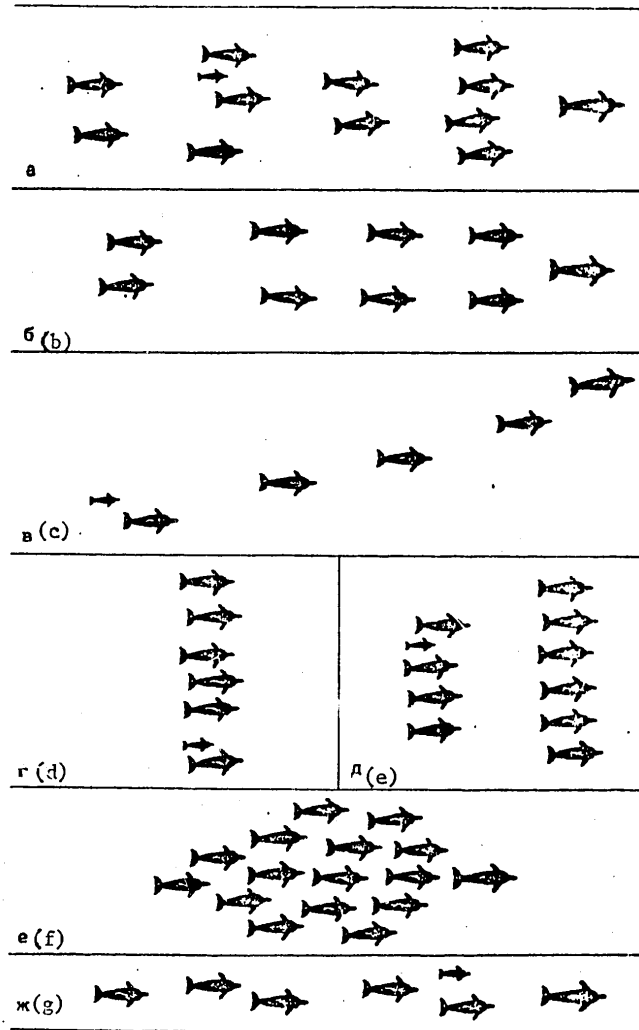


Figure 1. Formation Devices of a Herd of Bottlenose Dolphins: a) "formation;" b) "team;" c) "echelon formation" ("direction-finding"); d) "front;" e) "double front;" f) "tight group;" g) "line"

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The group structure also disappeared during a diffuse search, but was immediately restored with an orientative reaction, just as was observed among belugas (Bel'kovich, 1960). The group of bottlenose dolphins is apparently based on family relations (the female and her young), although there is also information on male herds (Taylor, Saayman, 1972) among the Indian bottlenose dolphins.

Two types of spatial differentiation of the bottlenose dolphin herd may be noted, directly connected with orientation and navigation. These are, in the first place, the dolphin scouts--a group of two or three animals that examine the coastal water area at a varying distance from the herd (for more detail, see "Povedeniye pri okhote" [Behavior When Hunting]). In the second place--it is, apparently, the leader of the herd--the dominant dolphin. From the shore it has often been noted that the swimming herd is headed by one large animal or two animals. This picture was also noted from the air for bottlenose dolphins, and earlier for belugas (Bel'kovich, 1960). The dominant animal, seemingly, has ascertained the degree of danger, has inspected the "new thing," which is characteristic of the bottlenose dolphin in a tank and has been observed in the sea. For example, in a tank, two dominating females separated from the herd to go toward the danger (Bel'kovich, et al., 1969), and in the sea our catamaran was inspected by one large dolphin that swam 300-400 meters away from the herd and came up to within 15-20 meters of the catamaran. The group structure of the herd of dolphins was quite dynamic. For example, we observed a characteristic group, consisting of a female, young and one more large animal (nicknamed "Begemot") in the central part of a polygon consisting of a herd of 12 dolphins. Sometimes they were noted separately. In the eastern part of the biopolygon, this group hunted near the shore for several days, and the rest of the herd was not there.

Dynamics of the Structure of Groups and Herds

If one traces the composition of the groups found over a period of three seasons, certain conformities to principle are discovered: in season I, groups of three dolphins with one young dolphin and a group of four dolphins with one young dolphin were often encountered. If one examines the structure of the herds that pass through the biopolygon in season II, one sees that most often groups of three and five animals were observed (Fig. 2). The groups of three animals were with a young dolphin, or simply made up of three adult dolphins. The group of five animals consisted of two young dolphins and three adults. Since we observed this type of groups throughout the entire season, this to some extent indicates their stability, at least over a period of several months. The group structure of the herds in season III was characterized by the predominance of groups of two and three animals. The group of five animals (three adults and two young) in season III was not observed. The reasons for the change in the number of dolphins in the group (Fig. 3) may be related to the period of estrus, birth, or on the contrary, death of the young, young dolphins reaching sexual maturity, cooperation in hunting, etc.

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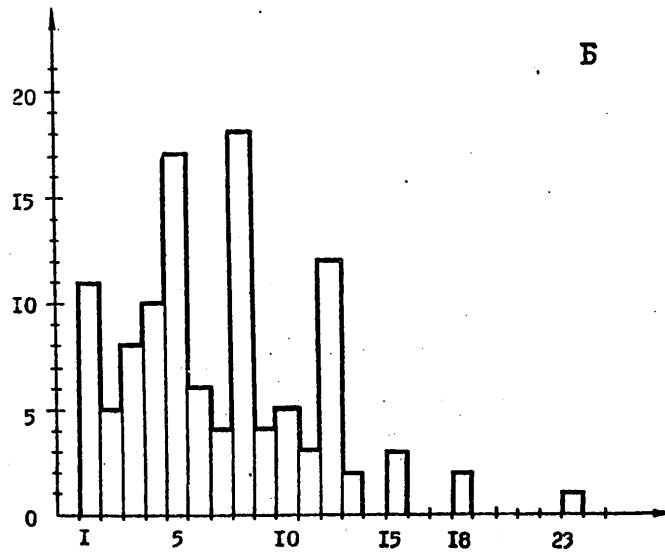
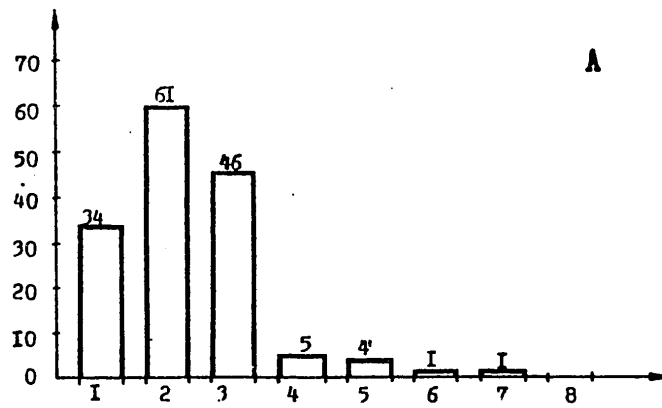


Figure 2. Degree of Encountering Groups of Bottlenose Dolphins of Varying Numbers (season III). A--NP-1, B--NP-3 and NP-4

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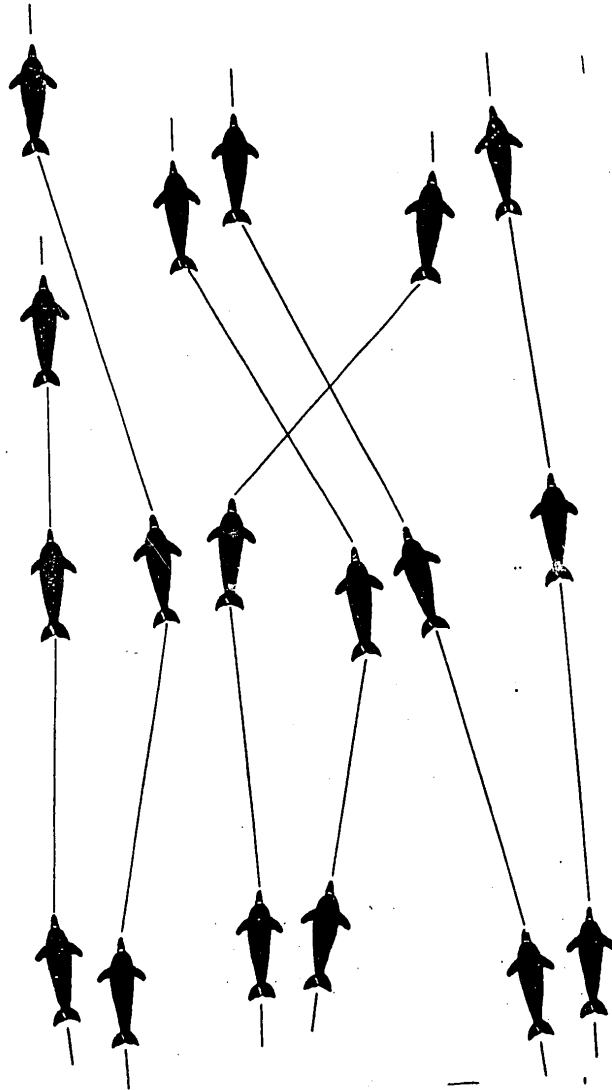


Figure 3. Shift in Composition in Groups According to Observations From a Catamaran

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The questions that are central ones for us are those of the uniformity of the basic composition of the groups (unit), the stability of the number of groups in the herd and, thus, the stability of the herd as an element of the local population.

Description of Specific Herds From Observations of Three Seasons

In order to identify the herds and groups of bottlenose dolphins swimming through the biopolygon, we directed particular attention to the following features:

1) The total number of the herd; 2) the number of groups and their position in the herd; 3) the number of young dolphins and their arrangement in the groups; 4) the coordination of the groups when hunting; 5) the characteristic behavior of individual animals; 6) the presence in the herd of animals with natural markings.

Here it should be noted that sometimes we observed the uniting of several herds into schools--at that time we noted 20-30 animals in this school, while as an example of a "real" herd, according to our observations for three years, there were no more than 13-15 animals. The schools were observed very rarely and usually formed and broke up during the period of a single observation.

Observations of Season I. In season I groups of two or three dolphins were observed in the overwhelming majority of cases. The relative density of other groups dropped sharply with an increase in their numbers. Cases were noted when, while the group of scouts was passing near the coast, far off in the sea the herd was observed, and sometimes later on it joined up with the scouts. Since the herd of bottlenose dolphins in season I rarely approached the shore, it is impossible to judge their number according to the data from season I.

Observations of Season II. In season II the herds came much closer to the shore than in season I. In the overwhelming majority of the passes, herds numbering from 3 to 12-14 animals were noted. When a comparison was made of the average size of the herds at the beginning and end of the season, an increase in it was noted toward the end of the season ($p < 0.05$). The data from season II make it possible to assume the presence of two herds of bottlenose dolphins in the observation region. The size of the first herd reached approximately 12 animals by September-October. There were only two young dolphins in the herd, and a group of four dolphins constantly followed the herd--one young dolphin and three adults. When in motion, this herd kept together more compactly than the second one. On 17 and 19 September an animal with a marking on the dorsal fin was noted in the first herd (Fig. 4a). The second herd of bottlenose dolphins reached the size of 13 animals by September-October. It had three young dolphins, and an adolescent was sometimes noted in it. In this herd a group of three

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adults and two young dolphins was singled out. The groups in the second herd kept themselves more aloof and were traced more clearly. A dolphin with two white stripes on the left side of the dorsal fin and two white spots on the right side was found in this group (Fig. 4b). It was noted for the first time on 27 May in a herd of six animals, where two females with young dolphins were observed. The marked dolphin had no young with it. Then, this dolphin was found on 2 August in a herd of 8-10 specimens (2 young), and on 14 September and 28 October--in a herd of approximately 10 specimens (3 young). On 31 October and 2 November it was noted in a herd of 9 specimens with 1 young dolphin. The second marked dolphin was recorded on 17 and 28 October in a herd of 13 specimens (3 young) and on 31 October in a herd of 9 specimens. In the last two instances it was together with the above-described marked dolphin.

The consolidation of the herds of bottlenose dolphins by autumn may be connected with the more compact arrangement of the groups (Fig. 5). At the beginning of the season the herd, apparently, was more dispersed, and not all the groups could be noted by the observers. The second possible variant is that new groups gradually merged with the herd, which before this time had existed independently or had been included in another herd. The data from season II do not make it possible to lean toward either point of view. It should be noted, however, that the somewhat greater spread of the size of the herds at the beginning of the season (Fig. 5) shows that at this time the herd was more dispersed. The change in the sizes of the herds at the beginning and end of the season indicates that the groups of bottlenose dolphins sometimes join and then disperse.

Observations of Season III. In season III the "peaks" in the size of the groups of dolphins were characterized by the figures: 1, 2, 4, 5, 8, 11. Having compared this with the data on the age composition, behavioral characteristics and results of the few encounters with marked animals, we could single out several herds of dolphins that constantly passed through the biopolygon.

In the western part of the central sector of the biopolygon, a herd of five animals was noted about 30 times. It was observed throughout the season, both from the shore and from the catamaran. In the herd was one young dolphin (it was not always noted when the observation was made from a great distance). One animal was singled out by its large size, as compared with the others. It was the first to approach the catamaran, and often swam in front, particularly when a hasty retreat was made. An animal with a white spot on the dorsal fin was noted twice in this herd. There were almost always two groups in the herd. In motion, great stability of the formation was observed in the group of three animals with the young one. The large dolphin was in the group of two animals (Fig. 6). Observations of the group structure of the herd of five animals showed that the groups had a certain tendency toward stability of composition.

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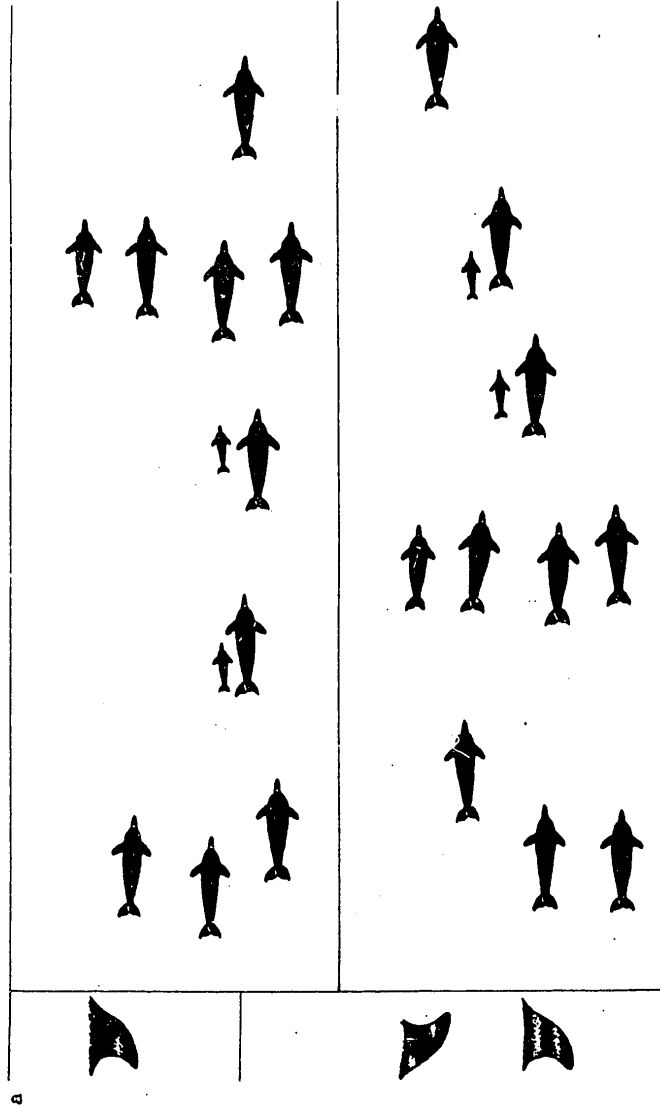


Figure 4 [Caption on Following Page]

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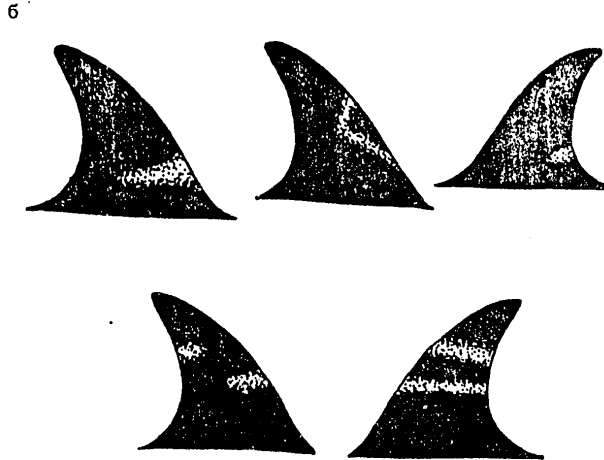


Figure 4. Formation of Herd of Bottlenose Dolphins Observed in Biopolygon on 17 and 19 September (Season II)

In the central part of the biopolygon we can single out three herds, the characteristics of which are given below.

Herd I was observed during the period from 6-16 July. A detailed description of the herd was obtained on 10 August, when there were four passes in a day, recorded by different observers, the descriptions of which are similar. The size of the herd was 10-12 animals of which 2 were young animals. On this day a typical example of the herd's motion "in a spiral" during the hunting time was observed. Another detailed observation of this herd was made on 14 July, in a "march" passage (peaceful motion without hunting) (Fig. 7). Just as on 10 August, three pairs could be singled out. One large dolphin moved ahead of the herd, with the distance between it and the first pair being constant. A group of three dolphins closed up the herd: two adults and a young dolphin between them. It was usually observed that the young dolphins, during the hunt, were with the adult animals and their position in the herd was fixed. In this herd were two small dolphins, which behaved completely independently during the hunt. For example, on 10 August, after the regular hunt, one of the young dolphins swam approximately 20 meters in front of the herd, striking with its tail, turning over first onto its abdomen, and then onto its back. There was about 10 minutes constant distance between it and the rest of the herd.

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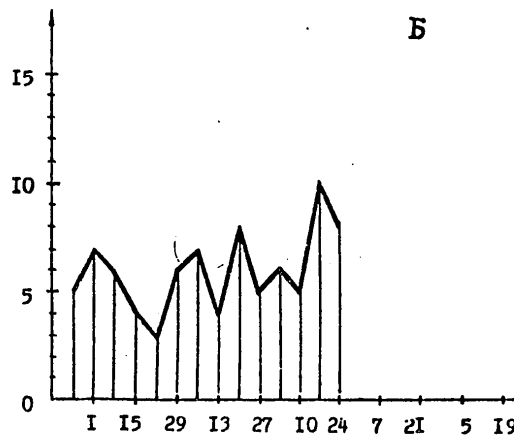
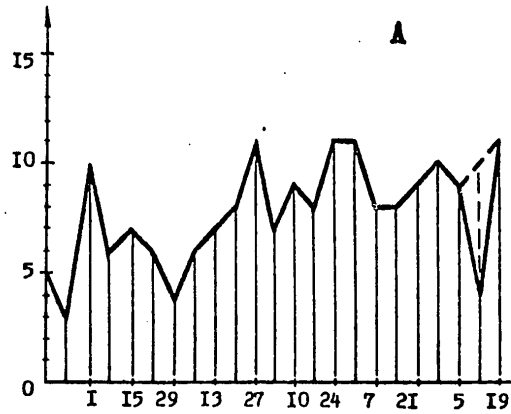


Figure 5. Variability of the Size of the Herd of Bottlenose Dolphins (on the Average for a 7-Day Period) in Seasons II (A) and III (B)

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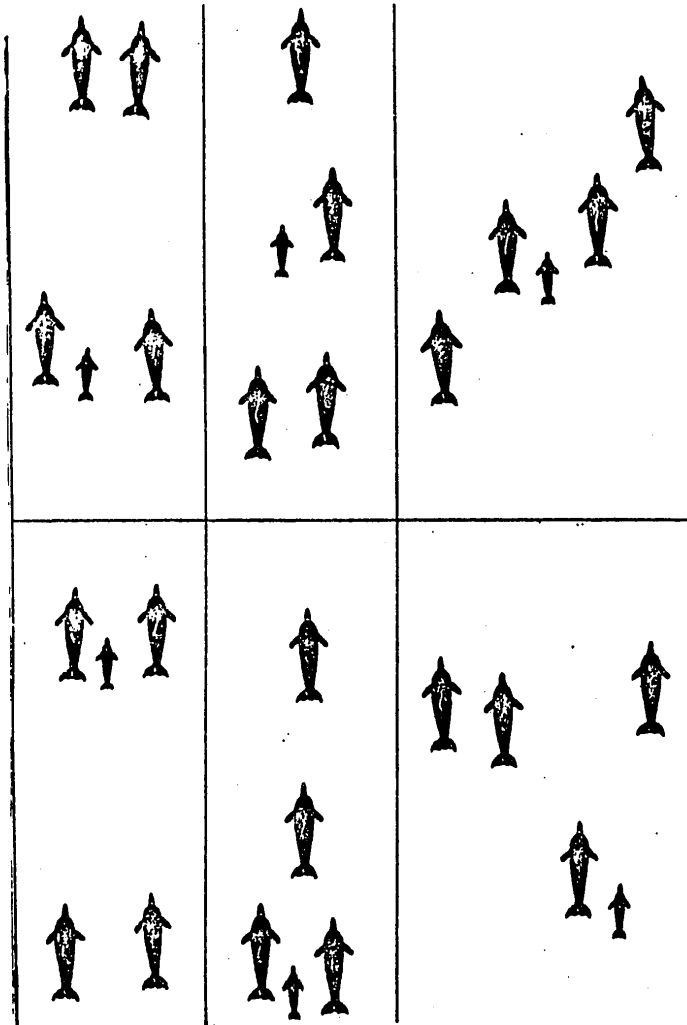


Figure 6. Formation Devices of a Herd of Bottlenose Dolphins of Five Animals (Season III)

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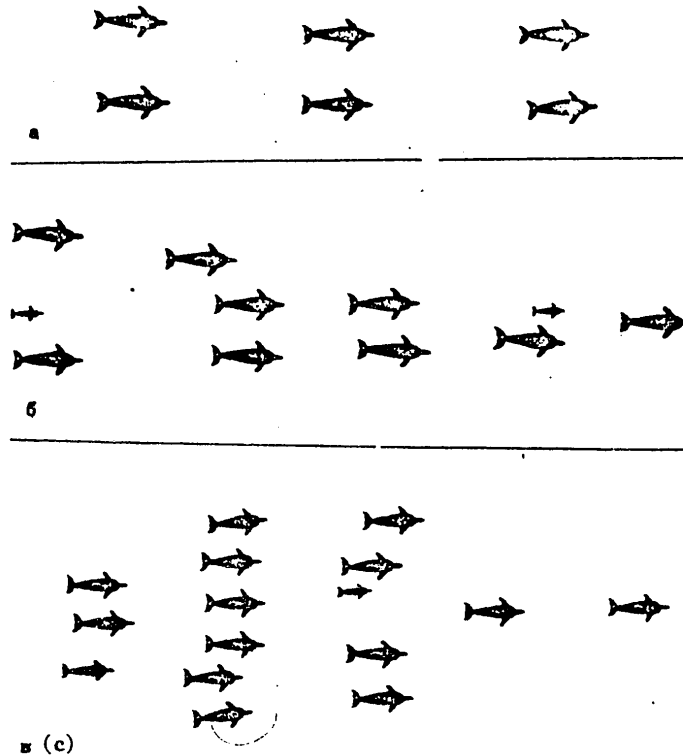


Figure 7. Formation Devices of a Herd of Bottlenose Dolphins

On 12 August there was a group of 6-7 bottlenose dolphins in the biopolygon, separated during the hunt in the following manner: group I--two adults, group II--two-three adults, group III--two young dolphins. During the hunt groups I and II were 200-250 meters away from each other, and group III, consisting of the two young dolphins of identical size, was in the middle. This arrangement of the dolphins continued for about 50 minutes. The behavior of the young dolphins could be estimated as play: constant leaps, "vertical climbs," and momentary flashing of heads and tails; the respiratory pauses in this case were not over 5 seconds. Once every 5-7 minutes an adult dolphin surfaced near the young dolphins and then disappeared again. Supported by this characteristic independent behavior of the two young dolphins, we feel that these six-seven dolphins should be regarded as a group of herd I. The dolphins

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observed earlier, on 12 and 13 June, probably belonged to this herd I. About 10 animals, of which 2 were young ones, were counted in the herd. "Tandems" were characteristic of the formation, and a group of three dolphins closed up the herd: two adults and young dolphin between them.

Herd II was noted in periods following each other: 17 and 18 August, 20 and 21 August and 8, 25 and 30 September. The herd came closest to the shore on 20 August, when its number was determined to be 15-17 animals. The "march" formation of the dolphins is shown in Figure 7. Three groups were clearly singled out, and the distance between them was 30-50 meters. In this herd was one young dolphin and one small-sized animal, possibly an adolescent. One large dolphin moved in front of the herd, and behind it, one or two dolphins (it was not possible to establish clearly by the nature of the surfacings). In this herd two of the animals had the characteristic features in the body structure (Fig. 8). A sharp fluctuation was observed in the size of the second herd. On 8 September a marked dolphin was observed in it, which was encountered in the preceding seasons. It was in the herd where the group of five animals was observed. Later this group was not observed in the herd with the marked dolphin. This makes it possible to assert that among bottlenose dolphins, groups preserve a constant composition only at a certain time, just as among other dolphins

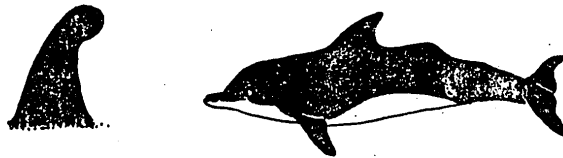


Figure 8. Characteristic Features of Two Dolphins of Herd II of the Central Part of the Biopolygon

(Bel'kovich, Yablokov, 1963). Obviously, the birth of young and the sexual maturation of dolphins lead to a change in the old and formation of new groups. At the end of August and in September, three groups were quite clearly singled out in the herd. In one were two or three animals, and in the two others--approximately six each. On 28-30 September, this herd with the marked dolphin and one young dolphin again numbered up to 8-10 animals. In these two periods there were brief observations of 5-6, 9-10, 1 and 2 bottlenose dolphins. Apparently all these dolphins belonged to the second herd and were its groups. Up to 17 August, when herd II appeared for the first time, for a week there were no dolphins in the biopolygon; on 24 August a new herd appeared, which differed sharply from the second.

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Herd III was observed on 24-26 August and 29 September; it consisted of 8-10 animals. There were three passes of this herd, and each time an intensive hunt was observed, and therefore the "march" formation for herd III remained unknown to us. During the hunt the dolphins dispersed over a large area. The number of animals during each of the three passes gradually increased. A group of four animals (one adolescent) was singled out in the third herd. The group was divided into two pairs, and in one was a dolphin with a crescent-shaped fin. The most characteristic feature of the animals of this herd consisted of bright sections of skin. It may be assumed that the dolphins had a skin disease or that such pigmentation is inherited, and the animals were related to each other. Four dolphins of this herd are shown in Figure 9. The marked dolphins could be clearly seen during each day of this period. Since most of these marked animals from NP [observation post]-1 were not seen, it may be assumed that this herd appeared in the biopolygon in season III only in August for three days. However, the group of four dolphins which contained the adolescent and the animal with the crescent-shaped fin was very similar to the local group of bottlenose dolphins of the eastern region of the biopolygon (see below). The dolphin of herd III shown in Figure 9b joined another pair of adult dolphins from the same eastern region in the biopolygon. One of the observations of this herd on 25 August clearly showed that the herd of bottlenose dolphins may disperse over a large water area, and therefore was not always considered as a whole. At 1205 hours a herd of eight animals was noted in the western part of the biopolygon from the catamaran. After 20 minutes the herd passed by NP-3, where eight dolphins were observed. Only five animals could be seen from NP-4, and at first, from NP-1--2, and then, at a great distance from them, another one (at 1303). At 1350 this herd was noted in the eastern part of the biopolygon, moving backward, and after 1400 hours, all eight-nine dolphins were again at NP-1 in the central part of the polygon.

In the eastern part of the biopolygon in season III, observations were made for 32 days from 4 June to 9 August, and bottlenose dolphins were noted 66 times (see Table 1). One group of four bottlenose dolphins constantly inhabited the region of the observations. Studied in greatest detail was a bottlenose dolphin measuring 1.5-1.7 meters, judging by all signs--a nonmatured specimen aged 1.5-2 years, called "Podrostok" [adolescent]. Fifteen observers saw the adolescent and their descriptions are similar. The animal had characteristic markings on the body and with each observation from one to four such markings were recorded. The overall coloring of the animal was light gray; directly behind the rostrum on the frontal projection there was a bright spot with blurred edges. A white scar about 15 cm long passed from the blow hole to the dorsal fin. The largest part of the scar (10 cm) passed in the middle of the back, and then turned off steeply toward the left side. On the right side, behind the dorsal fin, askew, was another light gray scar, as if stitched with small stria stitches. The top of the caudal pedicle was speckled with small scars resembling traces of the teeth of bottlenose dolphins (Fig. 10a).

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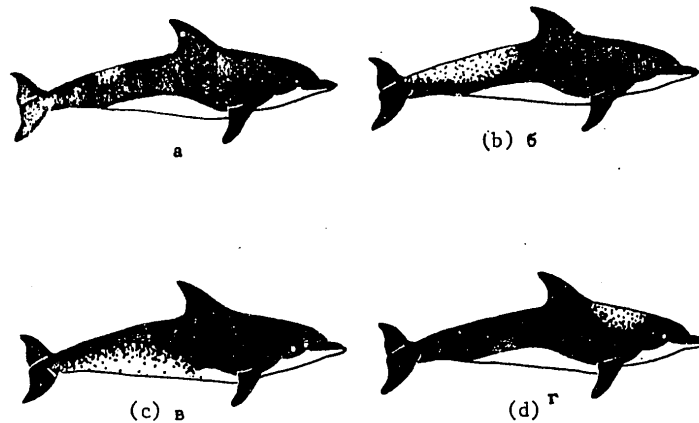


Figure 9. Dolphins of Herd III of the Central Part of the Biopolygon With Characteristic "Marks"

Table 1

	Number of Observations		
	Total	Including with young	Including reliably observed "adolescent"
1	16	6	3
2	18	9	3
3	16	13	8
4	12	12	7
5	2	2	2
6-7	1	4	
3	1	1	
Total:	66	47	23

"Podrostok's" partner was a large, dark bottlenose dolphin with the characteristic high, narrow crescent-shaped fin, called "Sekator" (Figure 10c). At first, often only one partner was recorded, and the second was noticed later. In observing the group of four bottlenose dolphins it was noted that "Podrostok" or "Sekator" kept together, but this pair was

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not as stable as the second pair of bottlenose dolphins. Two large adult animals approximately identical in size formed the second pair. The characteristic feature of one of them was a light round spot on the caudal pedicle and a caudal fin, whitish on the left side, as if scratched (Fig. 10 b, d). This marking was recorded four times by five observers. The second dolphin of this pair had quite a high sharp fin (not, however, of a shape similar to "Sekator's"), with a small bright spot on the right part (Figure 10d).

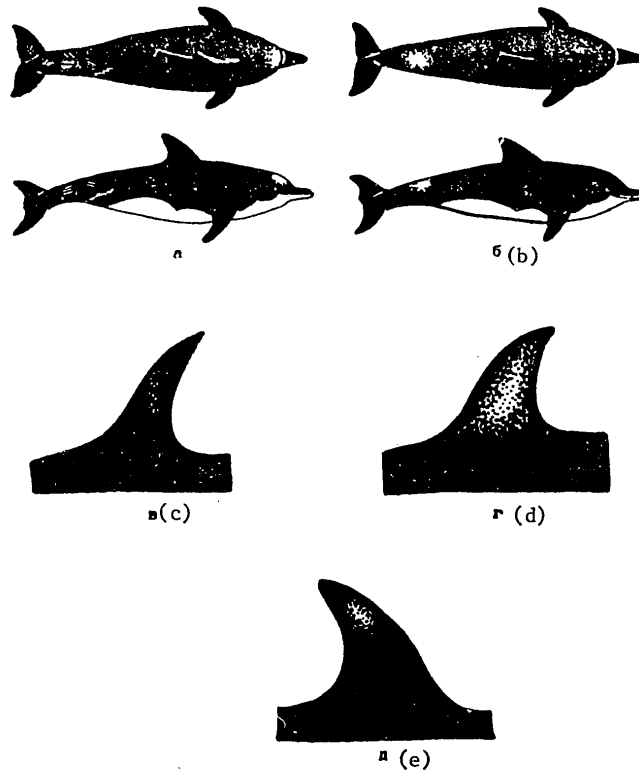


Figure 10. Bottlenose Dolphins With Characteristic Features in the Formation--"markings"--from the Eastern Part of the Biopolygon. a--"Podrostok," c--"Sekator." For Explanations, See Text

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The bottlenose dolphins appeared at varying times throughout all the daylight hours from 0500 to 2030 hours. Most often the animals were observed during the morning hours (0500-0900-27 times) and only one-tenth of the recorded passes were made after 1700. The types of formations of the group of four animals when they were moving are shown in Figure 11. When hunting or investigating the bay in search of fish, the dolphins separated into two pairs (Fig. 11a). "Podrostok" or "Sekator" often separated from this group, but not once was it noted that one of the dolphins of the second pair separated (except for cases of intensive, diffuse hunting, when the formation was completely disrupted). Three of the animals remaining in the group had the following types of formations (Fig. 11, f, g, h, k). In many observations, initially only one dolphin--"Podrostok" was noted, and it would disappear after a while and then again appear with "Sekator," and again after a little while the second pair of dolphins would also swim up from the sea. The impression was thus created that "Podrostok" would seemingly "lead" the other members of the group from the sea.

We wondered how contact would occur among the local group of four dolphins described with other dolphins (and whether this contact took place). Four times we observed more than four dolphins in the water area at the same time. For example, on 10 July a herd of 8 bottlenose dolphins passed, consisting of groups of 3 and 5 dolphins (Fig. 11, k, i). This herd came no closer to the shore than 400 meters and, probably, was not related to the group of dolphins being observed. On 16 July a fifth dolphin was twice noted in the local group described. It joined the second pair of animals (Fig. 11, m).

A single time (20 July), after emerging from the bay and moving along the coast to the central part of the biopolygon, another 2-3 dolphins joined the 4 bottlenose dolphins. The group of 4 dolphins, however, was clearly singled out in the herd of 6-7 animals that had formed.

The animals described were not observed during the work period of NP-7 in the central part of the biopolygon. Later, however, on 25 August, and twice on 26 August, a herd of 8-10 bottlenose dolphins was observed from NP-1, and the presence of the characteristic markings--light spots on the body--was characteristic of them. Among the herd a pair of bottlenose dolphins was singled out, one of which had a round white spot on the caudal pedicle. Apparently, this was the marked dolphin from the second pair of bottlenose dolphins observed in the eastern part of the polygon (Fig. 10b). One of the dolphins of this herd had a different marking--a completely bright caudal pedicle. This animal was observed from the yacht on 4 August in the eastern part, 1.5 km away from the shore in a group of 3-4 bottlenose dolphins, moving in the direction of NP-1.

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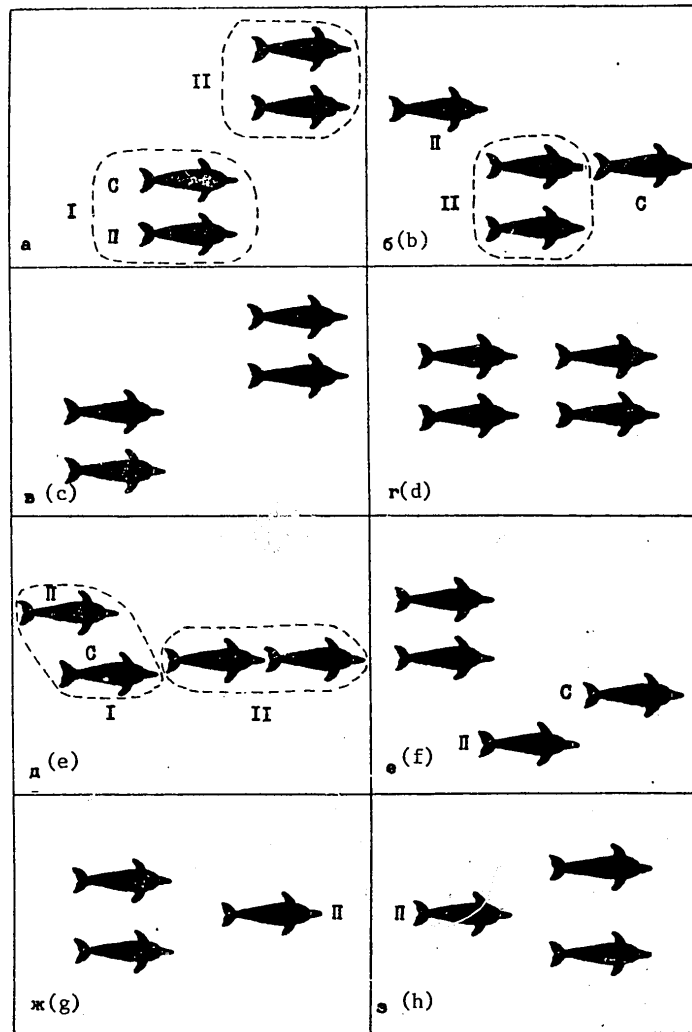


Figure 11. Nature of the Formation of a Group of Dolphins From the Eastern Part of the Biopolygon. Explanation in Text.

[Figure Continued on Following Page]

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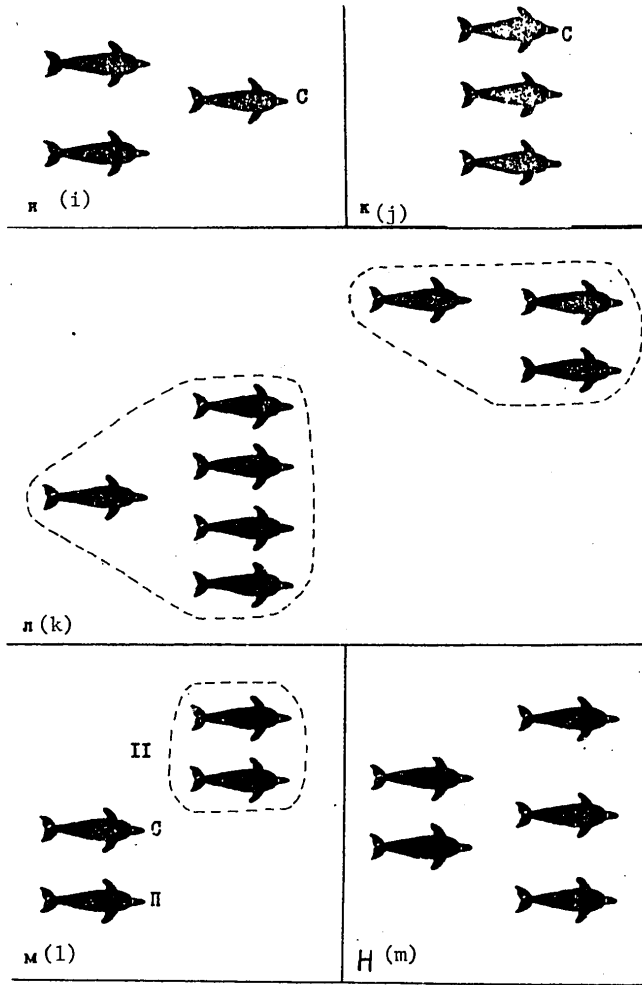


Figure 11 (Continued)

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On the basis of this it may be assumed that the group of 4 bottlenose dolphins described, constantly observed in the eastern section, was part of the single herd of bottlenose dolphins and maintained contact with it.

To complete the picture, it must be added that in the central section of the biopolygon, a solitary animal was noted six times from 12 August to 14 September. It would often remain in a small section of the water area for several hours, moving slowly through it. The behavior of the solitary dolphin differed sharply from the norm and did not resemble the behavior of a "scout."

From time to time larger herds were encountered in the biopolygon than described in this work, but these were obviously not actual herds, but schools. Such a school could be an accumulation of 15 animals (17 August-8 September). On 14 August a school of approximately 23 bottlenose dolphins was noted, which consisted of two parts: 15 and 8 animals. These parts moved several dozen meters apart from each other.

Porpoises and Common Dolphins

Azovki [*Phocoena phocoena* Linnaeus] porpoises usually appeared in the biopolygon singly (36% of the observations) and in small groups of two (32%), three (14%) and four (7%) animals; sometimes there were six-eight (7%) dolphins in the group, and in May of season II a school of 20-25 Azov porpoises was noted. In the group of two animals, Azov porpoises with a young porpoise were noted in three (10%) instances.

Solitary porpoises were rarely observed in the biopolygon. Under conditions of good visibility, usually several animals would plunge along at a distance of hundreds of meters from each other. The unification of groups into a single large one for combined hunting was repeatedly noted. The large group would usually break up again soon afterward. For example, on 17 July of season II a herd of eight porpoises would break up into groups of two or three specimens each, and would then form up again; on 25 July, five porpoises would separate into two groups and would then combine again into one, etc.

In the course of field season II we recorded several animals with natural markings--the shape of the fin of the marked porpoises was different from the ordinary triangular shape. Unfortunately, there were no repeated encounters with these animals. In season III, however, six times in a half a month (30 July, 5, 9, 11, 13 and 16 August), a marked porpoise was observed from NP-3 and NP-4. This was a youngster, with a jagged, scarred fin. It was often noted in the group with a larger dolphin (obviously the mother). Sometimes a third--the largest of them--was also noted together with these two porpoises. It behaved quite independently--sometimes it would swim away from the female with the youngster and even disappeared from the field of vision, and then it would come up again

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and move with them in the same direction. It is possible that this was always the same porpoise (it is impossible to say precisely, since it had no markings). On 5 August, mating was noted in this group of porpoises. In addition, three times in the course of the entire season a porpoise was noted whose fin differed somewhat from the ordinary triangular shape and resembled the fin of a bottlenose dolphin. These data make it possible to assume the existence of a local population of porpoises in the region of the southern coast of the peninsula.

Belobochki [Delphinus delphis Linnaeus] white-sided dolphins were encountered in herds numbering from a few specimens to several dozen. During the migrational movement, groups of two to four animals (sometimes of a single animal) could be clearly seen in the herd. In each group the dolphins would take turns jumping up, one after the other. These dolphins did not swim up close to the shore.

Conclusion

An analysis of our data on the size of the herds of bottlenose dolphins, the age structure, the structure of the groups and the behavioral characteristics, as well as observations of the marked animals, indicate that essentially the same herds of bottlenose dolphins or parts of these herds passed through the biopolygon.

The observations of season III of the year are considerably clearer than of season II, and indicate stability and permanence. The basic structure of the unit of population of the bottlenose dolphins is a group of animals united into herds, and an aggregate of herds forms the local bottlenose dolphin population. The herd of bottlenose dolphins is characterized by relative stability and long-term independent existence. The group structure of the herd of dolphins is a labile and finely tuned mechanism to ensure the optimum conditions for the spatial-temporal use of the water area, as well as adequate methods of hunting, given the changing conditions of the environment. Nevertheless, one may assume the existence of a constant "central" grouping--of one or several groups, which makes up the basis of the herd. To this basis, possibly, groups of dolphins may attach themselves. In addition, separate groups may separate from the herd, and begin to exist independently and provide the basis for a new herd. These very interesting questions of the dynamics of the population may be revealed in further studies.

The observations of the bottlenose dolphins in the Indian Ocean were mainly of an ecological nature, but at the same time it was revealed that the Indian bottlenose dolphins swam in schools of several hundred animals, and the schools consisted of distinctly expressed herds of 20-50 specimens each. These herds were often encountered separately from the school, as well. Groups of 2-5 dolphins each were noted in each herd, as among the bottlenose dolphins in the Black Sea. Also noted among the Indian bottlenose dolphins were animals with natural markings, which turned up in the

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region of operations in the course of several years (Taylor, Saayman, 1972).

Data on porpoises and common dolphins, unfortunately, are very meager. Observations of Azov porpoises, however, provided interesting material on the structure of the herds and showed the possibility of local dispersion of individual subpopulations of this species.

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UDC 591.513

DESCRIPTION OF THE SEARCHING-HUNTING BEHAVIOR OF DOLPHINS

Moscow POVEDENIYE I BIOAKUSTIKA DEL'FINOV in Russian 1978 pp 34-65

[Article by V. M. Bel'kovich, Ye. Ye. Ivanova, O. V. Yefremenkova, L. B. Kozarovitskiy, S. P. Kharitonov]

[Text] Our knowledge of the nutritional biology of dolphins, drawn from observations in oceanariums, is essentially not on a comparable basis with their hunting behavior under natural conditions. References to the hunting of various species of dolphins (porpoises, pilot whales, common dolphins, etc.) by surrounding the fish are made in the survey article by W. Evans and D. Bastian (Evans, Bastian, 1969). A. G. Tomilin (1957) gave an interesting and quite detailed description of the hunting of Black Sea bottlenose dolphins, which surrounded a school of fish, confused it into a "standing school," and consumed it. He also gives a description of the hunting of a group of bottlenose dolphins that backed fish up to the shore. D. A. Morozov (1970) also described this form of hunting among bottlenose dolphins. Quite a detailed description of hunting among Indian Ocean bottlenose dolphins is given in a special work by S. Taylor and G. Simon (1972), who note two types of hunt--by groups scattered along the coastal area and by a herd which drives the fish together into one spot and devours this school from the sides and from below.

Bottlenose Dolphins

Several hundred hunting situations were recorded during the work of our expedition. In this case the dolphins demonstrated great complexity and variety in their feeding behavior. At the same time, the dolphins, just as other animals, procured their food by using well worked-out procedures. Observations accumulated for several years of the hunting of dolphins make it possible to single out these standard procedures in the fantastic interweaving of elements of hunters' behavior. For example, in season I, small groups of bottlenose dolphin "scouts" would swim near the shore, and the herd appeared rarely in the biopolygon and most often suddenly, if the "scout" dolphins detected a sufficient quantity of fish (Bel'kovich et al., 1975). In season II the picture changed completely. We saw practically no "scout" dolphins of the model of season I--most of the time the entire

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herd hunted in the biopolygon, and moreover, with a completely different formation of the collective hunt. The group of "scouts" became a rare, sporadic phenomenon, but on the other hand, individual dolphins were often observed swimming to a distance of 100-700 meters from the herd, and sometimes even farther. These were not solitary dolphins, but were the "scouts of the season II pattern." Finally, in season III the dolphins again behaved differently. They would usually swim 300-800 m from the shore. Apparently, this was caused by the need to swim around the fishermen's stationary net, which was in the biopolygon in June-July. The bottlenose dolphins hunted as an entire herd, and moreover, from the second half of the year groups of "scout" dolphins were noted, who swam out far (2-4 km) from the herd. This year differed considerably from the preceding ones and gave a great deal of new material, due to which, from the results of three years of observations we could also compile the concept of the general conformities to principle of the behavior of dolphins when hunting.

A detailed analysis of the hunting situation made it possible for us to single out particular types of the dolphins' hunting behavior. These behavioral reactions were most often combined and, particularly interesting, would alternate even during a single hunt. This clearly demonstrated the plasticity of the exploratory reactions of the bottlenose dolphins, permitting them to react adequately to changes in such factors as the species, behavior and number of fish, the weather, the swimming environment, the behavior of people and many other factors, as well as to correlate all this with the number of dolphins participating in the hunt and with the coordination of their actions.

The following phases should be singled out in the hunt: 1) search, 2) detection, 3) capture. Since the detection of the fish is often difficult to separate from the capture of the fish, we will discuss two more phases of the hunt: seeking the fish and catching the fish. On the basis of the results of the research, the description of the types of behavior of bottlenose dolphins during the hunt is given in accordance with our classification.

Seeking the Fish

A. Seeking the fish as a herd. The hunt of the entire herd of bottlenose dolphins with a shift in the direction of the movement was observed in the following cases (See Table 1).

Just as the particular case of hunting behavior in phase 1 of the hunt (the search), the movement of the herd as a "front" along a straight line may be mentioned, which was noted (see Table 2).

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Table 1

Date	Time	Number of bottlenose dolphins	Date	Time	Number of bottlenose dolphins
Season II			Season III		
19.6.	6.23 - 6.54	5(2j)	6.6.	14.55-15.22	10-12
20.6.	11.05 - 11.38	9(2j)	9.6.	16.45-17.27	8-9
20.6.	13.40-14.45	9(2j)	19.6.	08.39-09.20	5
27.6.	05.30 - 08.30	10	12.6.	18.20-19.05	10-12
30.6.	12.10 - 12.35	8	13.6.	05.38-09.22	7
06.7.	07.50 - 08.20	6(2j)	13.6.	15.04-15.35	9
08.7.	12.01 - 12.17	7(2j)	9.7.	13.42-15.40	6
18.7.	07.12 - 9.16	8-9(1j)	31.7	13.05-13.58	8
18.7.	11.45 - 12.04	7	24.8	16.12-16.40	5-7
26.7.	11.00- 11.45	7-10(2j)	25.8	14.00 -	8-10
02.8	17.53 - 18.17	8(2j)	26.8	11.41 - 12.21	10-12
04.8.	10.05 - 10.27	4	26.8	17.24 - 17.51	8
17.9.	08.20 - 10.49	12			
17.10	10.30 - 11.00	8			

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When the herd made complex and purposeful movements in the sea and all its members acted in unison, moving in synchronism in a spiral or circle, the impression was created that the fish were being driven in. In movement "as a front" with a shift in the directions, the level of cooperation among the bottlenose dolphins was striking: the dolphins would come to the surface and line up on the surface of the water, and only after this would they all simultaneously disappear under the water. This was repeated many times in a row. The dolphins that surfaced first rocked like floats in various places in the waves; 15-20 seconds, or 30 seconds would pass before there would be visible in the water a clear-cut, straight line of dolphin backs and fins, and the next moment-synchronized submersion for 30-70 seconds. Such observations, however, could be related not only to the search, but also to phase II of the hunt, when the catch of small pelagic fish, for example, horse mackerels and sprats, occurred.

Table 2

Date	Time	Number of bottlenose dolphins
31.7. Season II	12.44-13.09	18-22
06.8. Season II	12.26-13.12	22
22.6. Season III	12.47-12.57	8-9
18.8. Season III	08.11-08.45	6
25.8. Season III	14.00	8-10

Much more often the search was carried out along a complex path of movement (see Table 3).

Table 3

Date	Time	Number of bottlenose dolphins	Nature of search
Season II			
22.6	12.47-12.53	8-9	In a spiral
17.6	11.55-12.35	6(1 _i)	In circles
19.7	10.11-10.53	32(4-5 _i)	In squares
21.7	12.22-13.15	11	In squares
4.8	08.51-09.10	6	Tacking (staircase)
19.8	11.50-13.15	13	(staircase)
17.8	10.53-11.22	8(1 _i)	(staircase)

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B. Group Search. Along with the search made by the entire herd, a group search was also made, when only part of the herd acted as a unified whole, and therefore the herd occupied a large area and its configuration changed continuously due to the movement of the groups of dolphins. This type of behavior was noted in the following cases (see Table 4).

The groups "combed" the water area, after setting a "bearing," and swam, formed into a "front," as well as toward each other, even though the latter should rather have been related to driving in the fish after its detection.

Also noted along with this was a diffuse search, when the dolphins would scatter throughout a certain water area and the trajectories of their movement were different (see Table 5).

Usually the hunt was of a dynamic nature and the different variants of the search for fish described by us could pass from one into the other. For example, the herd could swim into the bay as a "front," and then scatter into individual groups over a large water area. When one of the dolphins detected a fish and made jerks toward it (detection phase), and then made its catch, often the rest of the dolphins would swim up to him and would begin collective devouring of the fish.

C. "Scout" dolphins. The search for fish by "scout" dolphins is a specific type of group search. Due to the number of characteristic features, we single out this type of search as an independent one. Usually the hunt with the "scouts" looked this way. A group of 2-4 dolphins would be moving 20-300 m from the shore. There was a detailed investigation by this group of the coves (the trajectories of their movement repeat the curves of the shore), sharp changes in the speed of movement and also a shift in the respiratory rhythm: from 15 seconds during quiet swimming to 6 minutes during the start of diving--all this indicated the search for fish. Often the rest of the herd swam on a parallel course in the sea at a distance of up to several kilometers. When the "scouts" would find a school of fish, the herd would swim up and join into the hunt. Sometimes the "scouts" would detach themselves from the herd passing in the sea and would investigate the fishermen's stationary net placed in the bay of the biopolygon, and would then go back to the herd again. Accompanying the "scout" dolphins along the shore gave a great deal of interesting material as early as season I (Bel'kovich et al., 1975). The "scout" dolphins' search for fish was also noted by us many times in seasons II and III, although the "scouts" that were seen were different (see Table 6).

Usually the "scouts" investigated the shore and, of course, would eat up the fish that turned up for them. In this case, as a rule, the dolphin who swam closer to the shore would find and eat the fish. This was usually a gray mullet, which the dolphins would drive in to the shallows and force to the shore or to the surface of the water, not letting it go

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Table 4

Date	Time	Number of dolphins	Number of groups	Date	Time	Number of dolphins	Number of groups
Season II				Season III			
20.6	11.05 - 11.33	9(2j)	2-3	5.6	15.10 - 16.39	3	2
6.7	11.18 - 11.37	14(4j)	4	8.6	11.07	7	2
16.7	14.35 - 14.45	7-9	2	12.6	14.03 - 16.02	8	2
25.7	09.00 - 09.52	14(2j)	2	13.6	05.38 - 09.22	7	2
26.7	11.00 - 11.45	7-10	2	26.6	12.09 - 12.58	4	2
31.7	12.14 - 13.09	18-22	5-6	19.7	15.55 - 16.30	7	2
1.8	10.34 - 11.30	13	2	10.7	5.30 - 8.40	11	3
6.8	12.26 - 13.35	22	5-6	10.7	13.10	11(1j)	3
19.8	11.50 - 13.16	12-13	4	26.7	11.41 - 12.21	10-12	3-4
3.10	10.20 - 11.12	10	3	8.9	13.55 - 15.04	20	5-6
13.10	10.40 - 11.05	10	3				
28.10	10.38 - 10.56	11	2				
	13.25 - 14.15	13	2				

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Table 5

Date	Time	Number of dolphins
06.8.II	12.26-13.35	22
08.7.III	11.07-	7
10.7.	5.30-8.40	11
18.7.	12.40-	4
29.7.	09.32-10.02	12-15

sideways or down. This type of hunt we called the "attack on the shore" (Fig. 12). Therefore, the position of the "scout" dolphins is not equal both with respect to the amount of "work," and to the possibility of being satiated: the dolphin working actively was the one that had swum closer to the shore. It has so far not been reliably established as to whether a redistribution of the "roles" would occur among the "scout" dolphins. Another question: would one group of "scouts" be replaced by another? Due to many hours (up to 6-8 hours) of accompanying the "scouts" along the shore, in the course of which animals with natural markings (spots, scars, etc.) were observed, the idea was established that different dolphins appeared in the role of "scouts" (Bel'kovich et al., 1975), and consequently, there was no rigid specialization in the herd. Several observations gave grounds for assuming that the dolphins in the herd obtained information on the number of fish found by the "scouts" (Bel'kovich et al., 1975; Bel'kovich, Dubrovskiy, 1976). For example, on 27 June only part of the herd went up to the school of fish found. A herd of 13 dolphins was swimming by 500 meters from the shore. In the middle of the bay of the biopolygon, one large dolphin (scout) detached itself from this herd and swam along the shore. At the edge of the bay, alongside NP-1 he made an "attack on the shore," and caught a gray mullet, and immediately two more dolphins detached themselves from the herd and swam up to the "scout" and began to hunt along with him. After a brief hunt, these three dolphins attached themselves to the herd. We also noted a case when, upon detection by the "scout" dolphins of a school of fish, only three dolphins (two adults with a young dolphin) detached themselves from the herd, which was 2 km away from the scouts, and rapidly swam up to these "scouts."

Similar behavior is also described for the Indian bottlenose dolphins (Taylor, Saayman, 1972). One of the dolphins came across a school of sardines alongside the cliffs, and the entire herd of 200 dolphins, which was splashing in an area of 8 km², immediately drew together toward this spot and began the hunt. The authors assume that the dolphins could learn about the fish passively, since they could hear the echolocation signals of this dolphin.

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Table 6

Date	Time	Number of dolphins in herd	Number of scouts
Season II			
15.6	20.41-20.50	9	3
27.6	08.02-12.30	10	1
24.7	16.20-18.40	10(1, 1 j)	1
25.7	05.02-05.16	22	2
31.7	05.51-06.50	12-13(3j)	1
24.8	14.52-15.18	12-14	3
07.10	13.03-13.43	12	2
11.10	10.46-11.20	11-12	2
Season III			
5.6	15.10-16.39	-	3
11.6	12.33-13.07	8-9	1
11.6	09.10-10.44	-	3
12.6	18.20-19.03	10-12	
13.6	05.38-09.22	9-10	
4.8	13.43-14.23	10	
26.8	11.41-12.21	10-12	
31.8	08.55-09.11	-	

We discussed above various procedures used by bottlenose dolphins to search for fish. Since some of these procedures, for example, the movement of the herd, --in accordance with a complex trajectory in "squares," a "spiral," "stepwise"--we could not monitor acoustically due to the distance, we cannot completely unequivocally ascribe to them only the significance of a search. Moreover, in a number of cases these procedures were quite similar to the methods of catching small pelagic fish such as horse mackerels, sea carps, sprats and others. Since, however, the eating of the fish was noted neither acoustically nor visually, we so far relate these types of behavior of the bottlenose dolphins to search behavior.

2. Catching the fish. We will now discuss the concluding phase of the hunting behavior of the bottlenose dolphins, which ensured the catching of the fish. In this case it must be taken into consideration that observations in the oceanariums, when the dolphins eat defrosted fish, do not at all correspond to what takes place in the sea. The main

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difference is that the dolphin in the sea, in order to feed, has to move actively, and to be in close interaction with the other members of the group or herd. An analysis of our numerous observations showed that, given all the variety of methods of the bottlenose dolphins' hunting, the main prerequisite for catching the fish was restricting the mobility and maneuverability of the catch, which was achieved by various methods. We will discuss the principal ones of them in more detail.

a) "Carousel" and "boiler." When the herd was hunting for a catch in the sea of pelagic species of fish such as the horse mackerel, use was often made of the encirclement of the school of fish, taking it into a ring, which the bottlenose dolphins began to narrow gradually, swimming in a circle. This procedure was called the "horizontal carousel" and was very often noted (Fig. 13 (see Table 7)).

The number of dolphins that took part in the hunt of the carousel type could apparently serve as an indicator of the abundance of fish. So far we cannot determine which dolphins took part in this meal: the hungriest, the dominant ones, or simply those who found the fish (the most active? the most successful?). It is possible that they were actually the ones who found the fish, since for the herd as a whole the hunt did not stop with this. Sometimes several "carousels," following one after the other, were observed. For example, in season II they were observed: on 19 August--twice; on 19 September--three times; on 3 October--twice; on 6 October--three times; in season III--on 6 June--twice. It is possible that this was related to the fact that in some cases part of the school of fish succeeded in getting away from the encirclement, and in others--with the fact that the fish were in small schools.

Another type of fish catch was the "vertical carousel" and "boiler." They were most often observed after the "horizontal carousel," apparently when there was a considerable concentration of fish. The animals, having narrowed the circle, would begin one after the other ("carousel") or immediately, with several from various sides ("boiler") to dive inside the circle, into the accumulation of fish. These methods of catching fish were noted many times (Fig. 14) (see Table 8).

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Table 7.

Date	Time	Number of dolphins	Date	Time	Number of dolphins
Season II			Season II		
09.6	16.49	8-9	01.8	19.34	13
29.6	09.12	17(4)	17.8	10.57	8(1)
24.7	16.20	9-10(2)	18.8	07.45	8-10
31.7	05.51	12-13(3)	19.8	10.31	8
06.10	16.20	10	07.10	13.03	12
10.10	11.23	10			
Season III			Season III		
			10.7	18.51	8(1)
			04.8	13.41	10(11)
06.6	14.55	10-12	17.8	05.30	6(1)
12.6	18.20	10-12	24.8	09.42	5
10.7	05.30	11	25.9	08.31	13-15

As can be seen from these data, in both the hunt of the "vertical carousel" type and the hunt using the "boiler" method, sometimes part of the animals participated, which can be explained, just as in the case of the "horizontal carousel," by the small number of fish. The "carousels" of the two types and the "boiler" were characterized by rapid, impetuous swimming, noisy surfacing and a brief stay on the surface. It was not, of course, possible to see a small fish in the teeth of the dolphins, and if the object of the hunt was a gray mullet, often the bottlenose dolphins would jump out with the fish in their teeth.

D. A. Morozov (1970) described a hunt of the "carousel" type from observations made in the Crimea near the Kara-Daga cliffs. At first the school of bottlenose dolphins turned the head of the school, and the school began to swim in place. The dolphins, by twos and fours would swim up to the school of fish and, after having eaten their fill, would swim away. Approximately the same complex instance of organization of the hunt with the distribution of the "roles" among the dolphins was described for bottlenose dolphins in the Indian Ocean. Some of the dolphins ("guards"?) did not let the school of sardines leave the bay in the cleft of the cliff, until others swam up and fed (Taylor, Saayman, 1972).

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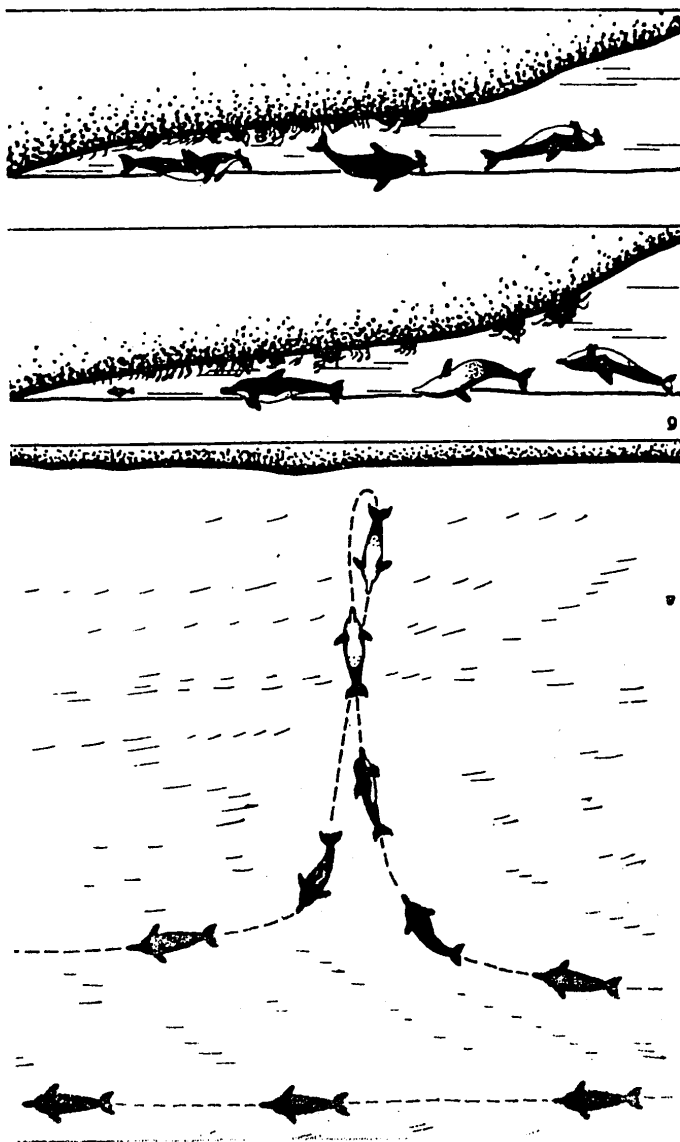


Figure 12. "Attack on the Shore," A--view from above, B--from the side

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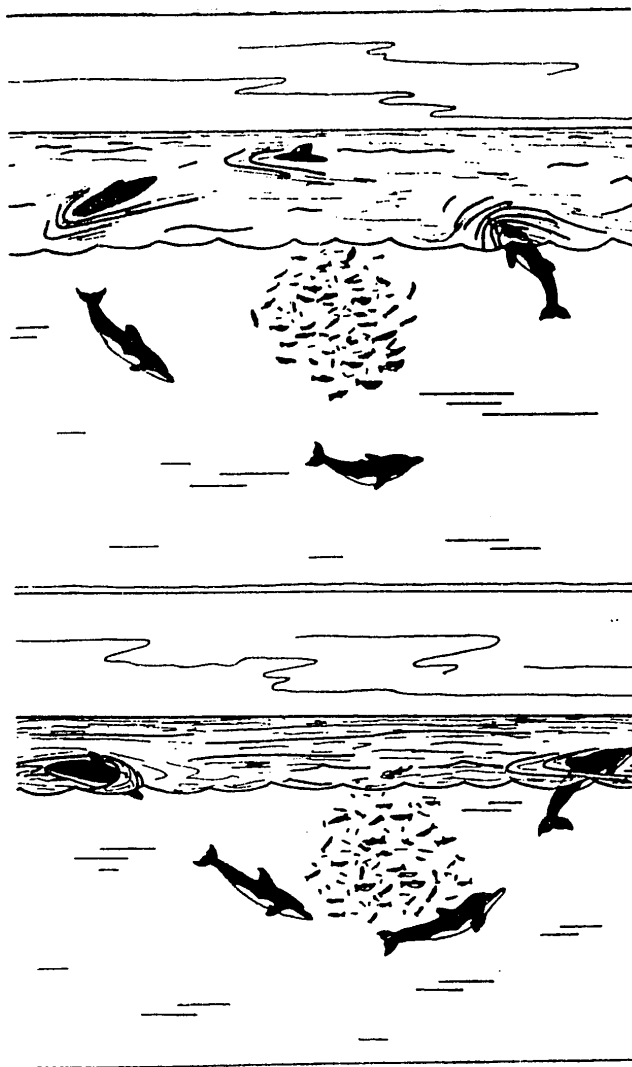


Figure 13. Schematic Depiction of the "Vertical" and "Horizontal" Carousels of the Bottlenose Dolphins

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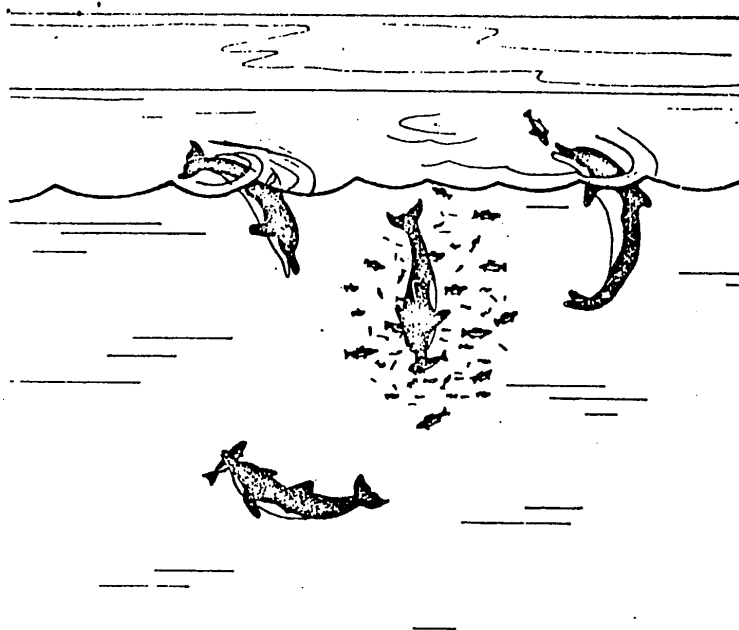


Figure 14. Schematic Depiction of the Catching of Fish by Bottlenose Dolphins, Called a "Boiler"

The "carousel" could be closed up (the bottlenose dolphins would swim in a circle, usually counter-clockwise) and not closed up. The "carousel" type hunt could be performed by the whole herd or part of it. The school of fish could be surrounded by several methods:

1. The dolphins would curve around the school of fish from one side and would close the ring with a "carousel" (6 October, 8 October (season II) Fig. 15).
2. The dolphins would encircle the fish from both sides simultaneously, and would take them into a "fork," after which the closed-up "carousel" was formed (for example, on 7 October (season II) Fig. 16). The dimensions of the dolphins' "carousel" would reach 150 m in diameter (12 June (season II)), but could be 50-70 m (6 June (Season III)) or even 25-50 m (17 August (season III)), which was most often determined by the initial area of the school of fish. As has already been noted, it might be that not all the dolphins in the herd would participate in the "carousel" (see Table 9).

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Table 8

Date	Time	Number of dolphins	Nature of Activity
1	2	3	4
Season II		"Carousel"	
6.8.	12.16	22(1j)	"Vertical carousel"
18.8.	06.35	8-10	3 "carousels" of 2, 3, 4 dolphins
24.8.	14.52	12-14	Same, of 2, 3, 5 dolphins
19.9.	10.35	10	"Carousel" twice
4G			
Season III			
05.6.	10.26	2	"Carousel" twice
05.6.	15.10	3	
07.6.	07.19	8	"Carousel"
09.6.	16.45	8-9	
10.7.	5.30	11	"Vertical carousel" of 5-6 dolphins
10.7.	16.15	8-10	Same, of 6-8 dolphins
16.7.	09.30	3(1j)	"Vertical carousel"
28.7.	11.12	2	

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Table 8 (cont'd)

1	2	3	4
---	---	---	---

Season II

"Boiler"

19.6.	5.06	5	"Boiler"
02.8.	5.38	7	
19.8.	13.05	15	"Boiler" of 8 dolphins
23.9.	11.56	10	"Boiler" of 4 dolphins
06.10.	16.25	10	"Boiler" of 3 dolphins
01.10.	13.03	12	Two "boilers," then three
13.10.	10.38	11	"Boiler"
17.10.	10.30	8	"
17.10.	14.56	8	"

Season III

06.6.	15.05	10-12	"Boiler" of 5-6 dolphins
09.6.	16.45	8-9	Several "boilers"
12.6.	14.03	8	Two "boilers" of 4-5 dolphins each
10.7.	13.26	12	"Boiler" of 4-5 dolphins
04.8.	13.43	10(1, 1j)	"Boiler"
20.8.	16.05	10-12	Two groups, two "boilers"
26.8.	11.41	10-12	"Boiler" of 6, then "boiler" of 3 dolphins
27.9.	07.45	8-10	"Boiler" of 5-6 dolphins
27.9.	14.20	12(1j)	

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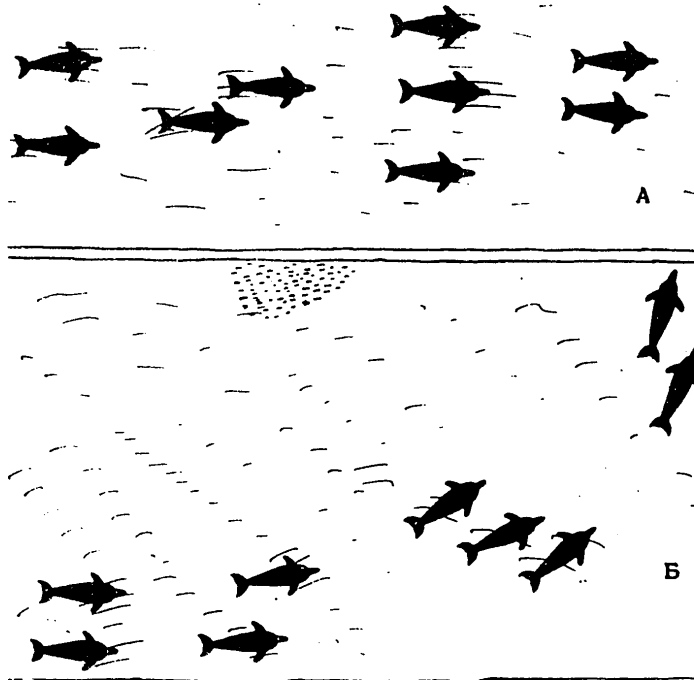


Figure 15. Schematic Depiction of Consecutative Phases (A-D) of Bottlenose Dolphins Encircling a School of Fish

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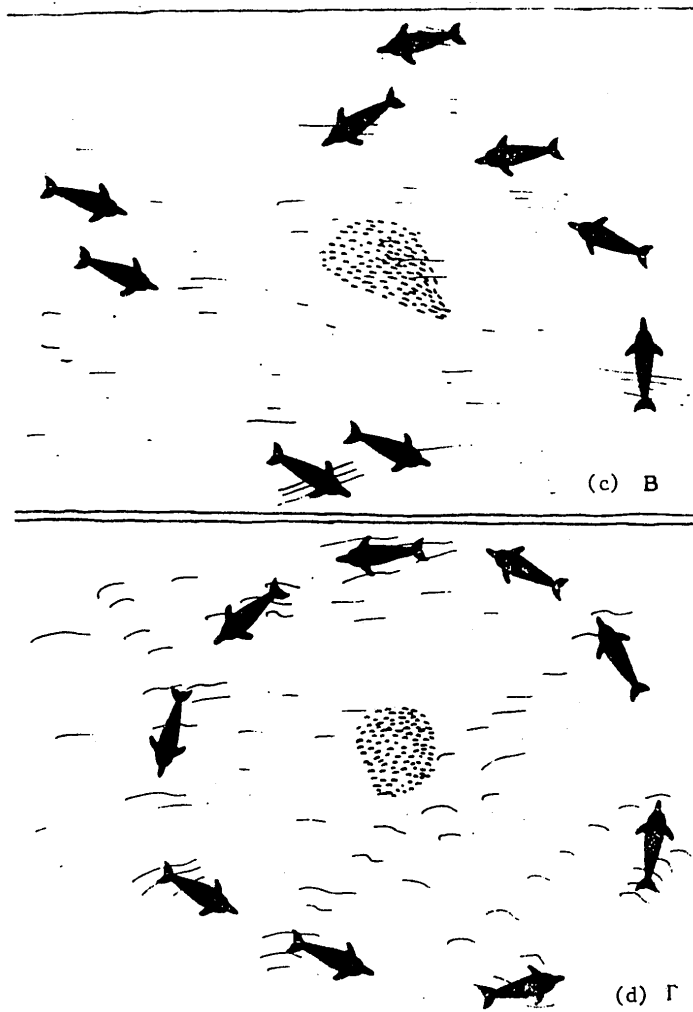


Figure 15 (cont'd)

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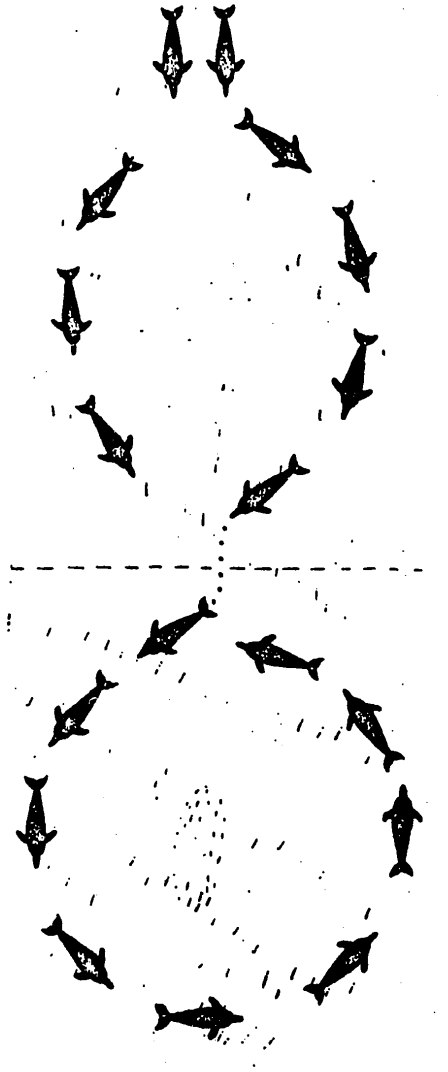


Figure 16. Schematic Depiction of the Envelopment by a Herd of Dolphins of a School of Fish in a "Fork" and "Carousel"

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Table 9

Date	Number of dolphins	
	Total	Participating in "carousel"
01.8.75 (season II)	13	5
17.8.75 (season II)	8(1i)	4
18.8.76 (season III)	8-10	4-6
19.8.75 (season II)	8	3-4; 7-8
07.10.75 (season II)	12	8

b) "The wall." In addition to the encirclement of the fish, the dolphins would use the device of driving the fish, for example, to the shore, or the nets placed in the water, or to a "wall" made up of one or several dolphins. One of these methods--driving them to the shore--was quite often practiced by bottlenose dolphins (Fig. 17C) (see Table 10).

Table 10

Date	Time	Number of dolphins	Nature of activity
Season II		Drive to the shore	
24.7	16.20	9-10 (2j)	"Front"
30.7	12.44	9	"Front"
01.8	10.34	13	"Double Front"
19.8	12.57	15	"Front"
17.9	09.29	12	3 groups of 3-4-2
19.9	10.20	8	2 "attacks" in a "front"
28.10	13.25	13	"Corridor"
Season III			
11.7	10.34	11	"Attack," 3 dolphins
28.7	11.12	2	Series of "attacks"
4.8	13.43	10	Entire herd; "in a front"

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The drive in to the enclosure might be participated in by the whole herd, which would most often line up in a "front," and sometimes--by individual groups. It is possible that this was determined by the species and number of fish. At this final phase of the hunt the dolphins moved rapidly, and caught the fish in the foam and spray at the very shore. For example, a hunt on 24 July (season II) was described as follows: "The dolphins fly completely out of the water, and more fly through the air than swim. The fish from a school of large gray mullets, which they are chasing, also fly completely out of the water and fly along for 4-7 m. Often the dolphins and the fish fly together, and sometimes the dolphins appear to be under a cluster of falling fish." In some cases (30 July (season II)), the school would prove to be large, and many fish would go off near the shore because they could not be caught. Therefore, cases were observed of a new drive to the shore (19 September (season II)).

It has already been indicated that a group of dolphins serve as a barricade for the fish. Therefore, it is expedient to present data on this hunting device as well, when the dolphins would use each other as a "wall" (see Table 11).

Cases were noted of a hunt of the "wall" type, when the bottlenose dolphins chased the fish to the shore in two almost parallel "columns"; here, apparently, both the shore and the parallel groups of dolphins were used as the "walls" (Fig. 17a). The dolphins were functionally equal, regardless of their number in the group, as when a pair of dolphins who, not having managed to press the fish near the shore (24 July (season II)), drove them to the herd and then the whole herd "as a front" pinned down the fish, or when groups approximately equal in number drove a school of fish against each other (for example, on 30 July, and 27 June (season II)), (13 June (season III)). Even one dolphin could fulfill the function of a "wall," since it inhibited the movement of the fish school or did not let a single large fish get away to the side. This was noted repeatedly in seasons II and III (see Table 12).

The wing of the stationary net was also used as a barrier to drive the fish into it. The group of dolphins in this case often drove the fish along the wing of the net to the shore. Some animals sometimes jumped over the net (26 May (season II)). (See Table 13).

c) Pursuit. As a form of capture by a group of dolphins and single dolphins we singled out the pursuit of the fish, when, without restricting the mobility of the school, the dolphins simply overtook the fish. Noted for the group of dolphins was pursuit "in a front" and "diffused," apparently with spawned fish in small schools, and this was also noted simultaneously, i.e., one part of the herd would pursue the fish collectively ("in a front," "on a course") and the other would swim separately at this time.

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Table 11.

Date	Time	Number of dolphins	Nature of drive
Season II			
20.6	11.05	9(2j)	2 groups
27.6	17.44	9(2j)	2 groups
24.7	16.20	9-10 (2j)	2 dolphins drive fish from shore to herd, and herd then drives to shore
25.7	09.00	14 (2j)	2 groups (4 and 4) and 2 groups (3 and 3)
30.7	12.44	9(j)	"front to front"
17.8	10.53	8(j)	triangle
19.8	10.31	8	"
19.8	11.50	13	2 "fronts"
19.8	12.52	15	2 groups
17.10	10.30	8	groups of 2 and 6 dolphins
Season III			
7.6	14.20	7	
9.6	16.45	8-9	2 dolphins drive fish to herd of 7 dolphins
13.6	5.38	9-10	"wall to wall"

Table 12

Date	Time	Number of dolphins	Date	Time	Number of dolphins
Season II			Season III		
5.6.	15.10	3	26.6.	12.09	4
6.6.	11.07	7-8	9.7.	13.42	6
11.6.	09.10	3	10.7.	05.30	11
12.6.	05.19	5	18.7.	6.07	6
12.6.	14.03	8	31.7.	5.51	12-13
13.6.	15.08	9	4.8.	13.43	10

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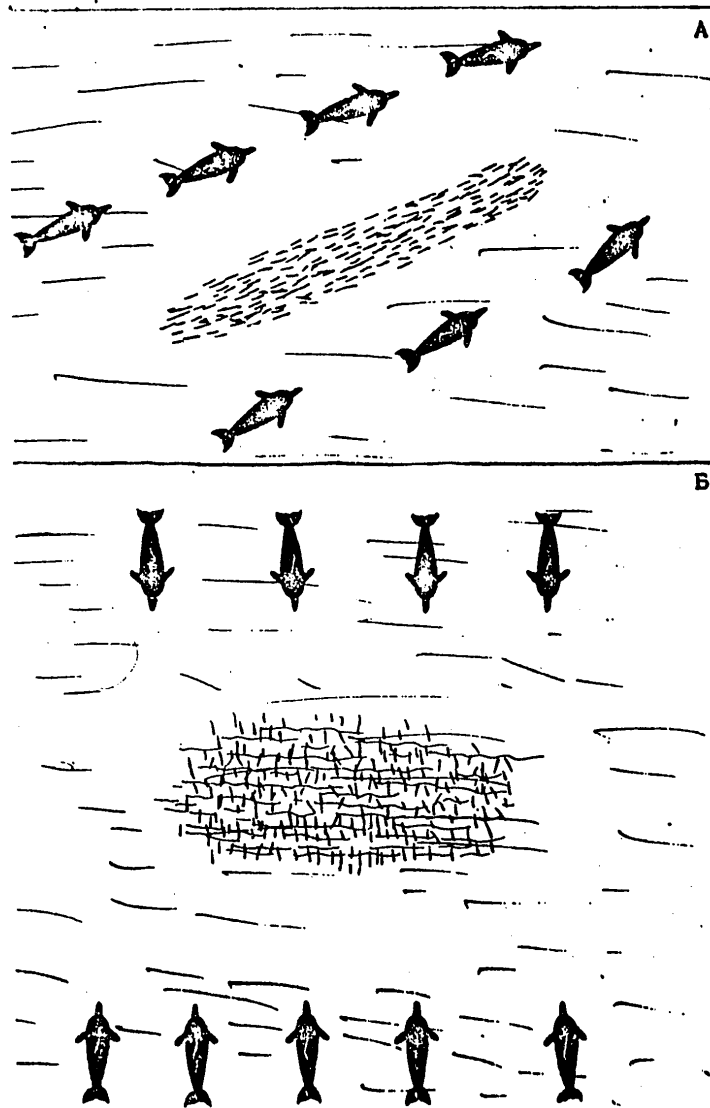


Figure 17. [Caption, Continuation on Following Page]

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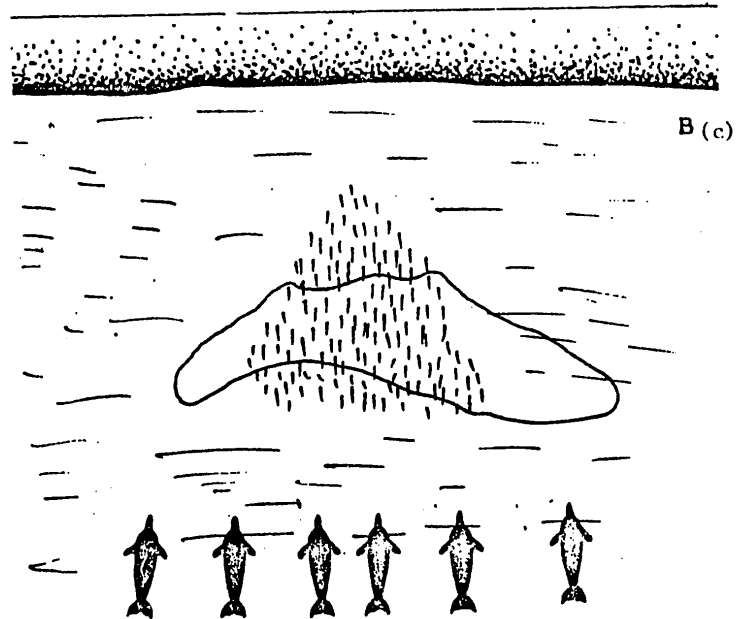


Figure 17. Schematic Depiction of Hunting Behavior of Bottlenose Dolphins, Driving Fish Against Barrier--"A Wall." A,B--between two groups of dolphins, C--toward the shore

Table 13

Date	Time	Number of dolphins	Nature of activity
Season II			
27.6	12.49	9(2 j)	2 groups
Season III			
8.6	11.07	4-5	In an "arc" and "front"
11.6	9.10	3	Alone and in group
11.6	12.33	3	"
12.6	14.03	8	"In a front" twice

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Pursuit of the fish "in a front" was noted in the following cases (see Table 14).

Table 14

Date	Time	Number of dolphins	Nature of pursuit
Season II			
27.6	5.30	10	"Front" with group of 3 dolphins
05.7	14.30	7(1j)	"On a course"
31.7	05.51	12-13	"Front" in a group of 5-6 toward shore, then in sea
02.8	05.38	7	"Front"
18.8	06.35	8-10	Rushes of 2-3 dolphins in synchronization
18.8	07.45	10-12	"Front" of entire herd in sea
19.9	10.20	8	"Front"

Pursuit "in a diffused manner" was also noted several times (see Table 15).

Pursuit "in a diffused manner" was also noted several times (see Table 15).

Table 15

Date	Time	Number of dolphins
Season II		
27.6	05.30	10
05.7	14.30	7
02.8	05.38	7
Season III		
26.8	11.41	10-12
17.8	14.27	2-3
08.9	13.55	20

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Characteristic of a herd's hunting "in a front," "in a spiral," and "in a circle" is the diving of the animals for a considerably longer time than usual--2-3 minutes. It appeared to us that this was connected with the natural localization of the food. This type of benthonic search (spawned fish) was also noted for other groups of bottlenose dolphins (see Table 16).

Table 16

Date	Time	Number of dolphins	Length of dive, min.
Season III			
7.6	14.20	7(2 gr.)	1
12.6	07.31	6(1-2 gr.) (3-4 gr.)	1-2 20 sec.
29.7	09.32	12-15	1-3
18.7	06.00	5-7	1.5-2

Hunting Alone

We discussed above the hunting procedures for a herd and groups of bottlenose dolphins. In these cases too, however, it would happen that the dolphin, although it found itself not far from a group of kinsmen, acted alone. It attempted either to drive the fish to the shore or to the wing of a stationary net, or to drive it up to the surface of the water. These are also variants of the "wall" type hunt, but only for a single animal. The data on hunting by a single dolphin using the "wall" method are given in the following table:

a) "Attack" to the shore (see Table 17).

b) We repeatedly noted the use of the wing of a stationary net as a "wall." In addition to this method of hunting, single dolphins pursued fish in a number of cases (see Table 18).

The most widespread procedure for hunting by a single dolphin is the "attack to the shore." The dolphin suddenly made a sharp change in the direction of its movement and rushed headlong toward the shore on the very surface of the water, with its dorsal fin thrust out of the water. At a distance of a few meters from shore the dolphin turned belly upwards and snatched the fish (most often a gray mullet), then immediately turned around and swam back (sometimes on its back), tossing up the catch once, or else two or three times, in order to grasp it again at the moment when

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Table 17

Date	Time	Number of dolphins	Number of "attacks"
1	2	3	4
Season II			
17.6	10.00	4	1
21.6	10.98	7	1
25.6	08.03	8	2
26.7	19.00		1
30.7	12.44	9 (2 gr.)	Several
31.7	05.51	12-13	"Attacks" of 2 dolphins
31.7	12.14	18-22	Several
3.10	10.40	10	1
Season III			
4.6	18.29		2
	18.33		
10.6	16.00	4	1
11.7	10.34	7-8	1
4.8	13.43	10	2
20.8	5.45	2	2

Table 18

Date	Time	Total dolphins
19.6 (season II)	16.55	8-9
12.6 (season III)	07.31	1
4.8 (season III)	13.43	4
24.8 (season III)	16.08	5-7
26.8 (season III)	11.41	10-12

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it came into contact with the water. Functionally, tossing the fish up ensured a convenient orientation of the fish for swallowing--head first.

What is involved in the procedure, constantly noted, of turning belly upward during the attack to the shore? Several ideas may be expressed with respect to this. One of them is that, under the conditions of shallow water, good light and clear water, the dolphin does not use the location apparatus. The fish are detected by means of the acoustic channel, and then during the pursuit and catch the dolphin uses its sight. Since its field of vision is directed downward, and the fish is overhead, near the surface of the water--it turns over, apparently to see it better. Another assumption is that the dolphin is protecting its pectoral fins from injury, and a third--it is more convenient this way to snatch the fish at the frons level. Most probably all of these and perhaps other reasons as well, operate simultaneously, because sometimes dolphins seize the fish in deep water too in the position "on the side," or "on the back."

Leaps When Hunting

Dolphins' leaps were often observed during hunting. Of the five types of leaps recorded by us among bottlenose dolphins during the hunt, only two types were noted:

1. A low horizontal leap (simple)--the dolphin jumped 30-50 cm out of the water in a steep arc (to a height no more than the thickness of the body from the surface), entered the water without splashes (Fig. 20b). Such leaps were particularly characteristic of the peaceful movement of common dolphins, and among bottlenose dolphins they were observed during rapid movement. Individual animals or a whole herd at once could leap, obviously when driving in the fish. It was these leaps that were observed during movement "in a line," with the entire herd jumping out in synchronization.

2. "Log" leap--the dolphins would fly out of the water at a slant and drop into the water flat. Often in this case the dolphin would thrust itself out of the water only with two-thirds or three-fourths of the body--the tail would remain in the water (Fig. 20d). Individual animals could leap like a "log," but more often--the entire herd. Such leaps were sometimes observed during the hunt; obviously, the dolphins drove the fish with blows of the body against the water.

"Vertical climbs" could be observed among the dolphins--vertical surfacing from the water with the head upwards and immediately--submersion on the vertical or with the fall on the side or on the back. This was often observed after a successful hunt, when many fish had been devoured. In the opinion of V. M. Bel'kovich, the possibility is not ruled out that the "vertical climbs" help to "shake down" the devoured fish in the belly.

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Some dolphins would make 5-8 "vertical climbs" each, in a row, in this case surfacing with the back along the course of the movement, and once 13 "vertical climbs" were recorded, with one vertical climb taking no more than one second.

Sometimes after the hunt, unusual submersions were observed, with up to half the body protruding from the water tail up. For example, on 14 July (season III), after the hunt, every third to fourth submersion of the dolphins was "tail up." V. M. Bel'kovich feels that perhaps, just as in the case of the "vertical climbs," in this case the devoured fish was being "shaken down."

Porpoises

It is more difficult to make a strict differentiation of the behavior of azovki [*Phocoena phocoena* Linnaeus] porpoises during hunting and migration than it is among bottlenose dolphins. The reason for this lies in the periodic long surfacings (up to 6 minutes) of these animals, during which they could swim far away from the former location, and the frequent hunting alone. Under conditions of good visibility and with only slight swell of the sea, however, such a classification proved possible. At the same time, the hunting behavior was much more easily identified than the migrational. The movement of the Azov porpoise consisted of a series of several dives (each one for 5-10 seconds), after which it would disappear under the water for 1-6 minutes, etc. During the clearly marked migrational movement, the Azov porpoises would move along a straight line at a speed of approximately 10 km/hour. During the hunt the animals moved more slowly (2-3 km/hour).

The slow movement of the animals through a water area several hundred meters in diameter served as a sign of hunting and searching behavior. Often during this movement, schools of ichthyophagous birds would follow the porpoises: small terns, cormorants and herring gulls. In some cases, however, the birds did not react in any way to the dolphins. In this case, apparently, search behavior occurred. The Azov porpoises could move through the water area during the hunt or search by several means. Most often the animals moved "like a shuttle" with varying range (Fig. 18). The animals often swam back and forth along the current belt, after diving a few dozen meters in one direction, after which they turned back. In a group of 2-3 specimens, the Azov porpoises moved in synchronization several meters from each other. Solitary porpoises during the hunt might make "loops" or move in a circle (Fig. 18, c, d).

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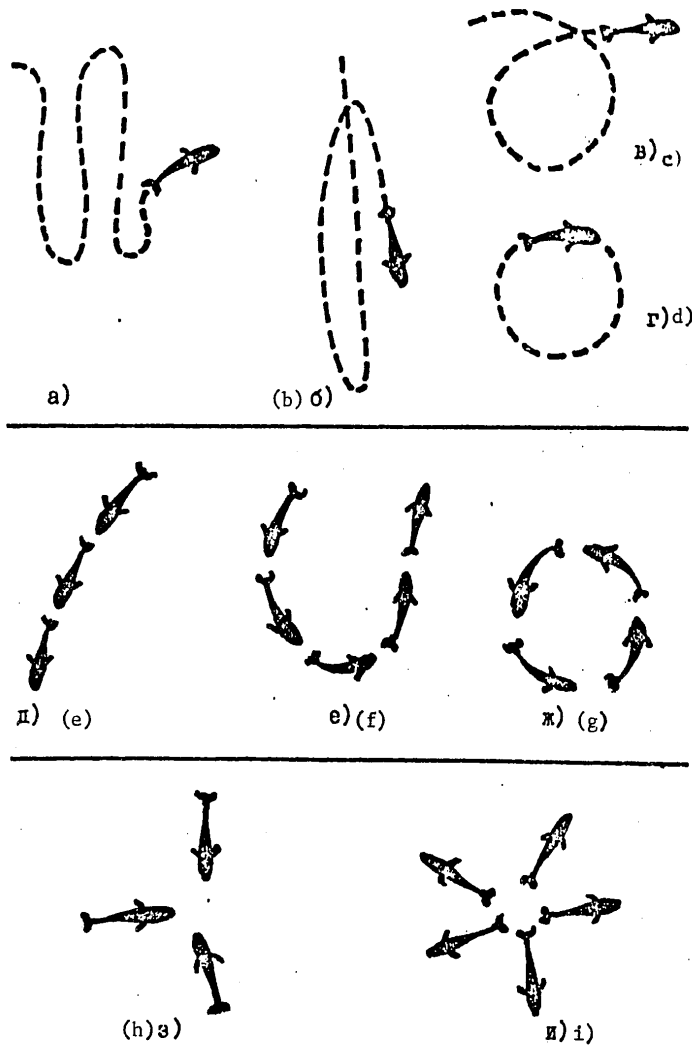
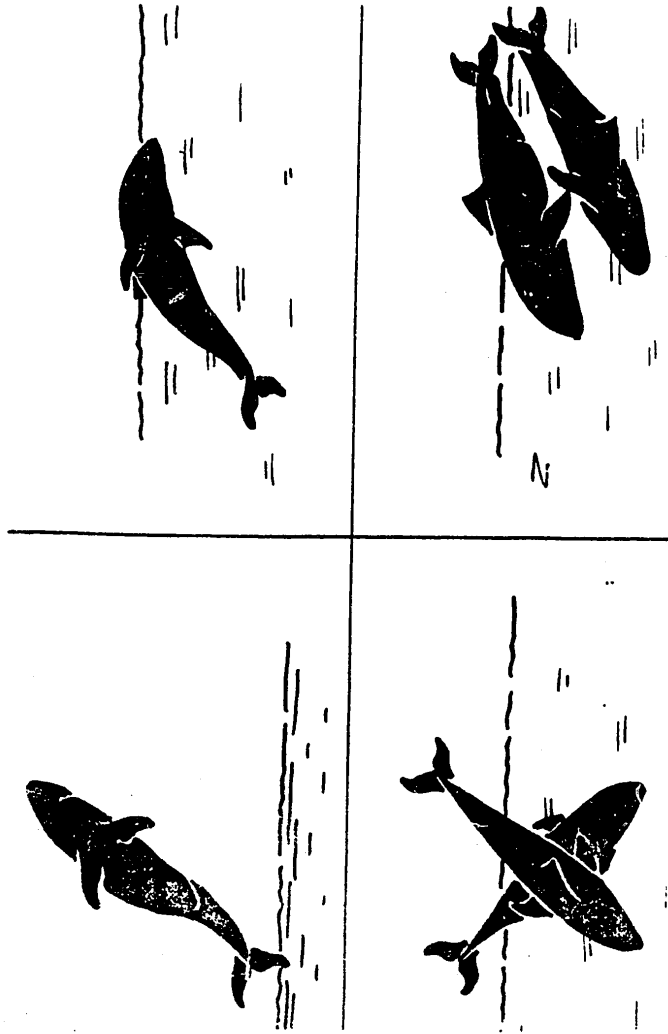


Figure 18. Movement and Hunting of Azov Porpoises: a) sinusoid; b) "shuttle"; c) loop; d) circle, e-g) carousel formation, h) boiler; i) "flower"

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Figure 19. Elements of the Sexual Behavior of Porpoises. Explanation in Text

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Sometimes more complex types of porpoise hunts took place--the interaction of individual specimens in groups was observed. As a rule the complex types of hunting were carried out by groups of 3-5 and more animals. Such a group might separate into two small groups, which would swim in "shuttle" fashion toward each other. For example, on 27 July (season III), three porpoises separated and one animal swam to meet two others, moving together. On 25 September (season II), we observed a group of six porpoises, which twice separated into groups of two and four specimens (possibly, to search for fish), and after a little while came together again. After the merging of these groups a new separation of a single animal occurred, who moved "like a shuttle" to meet the five. It is possible that the dolphins used this method to drive fish toward each other (in accordance with the "wall" type). "Carousels" and "boilers" of porpoises were noted repeatedly (Fig. 18 e, f). Sometimes the surfacing of several animals from the same place in diverging directions was observed (Fig. 18, h). On 5 October (season III) a "wall" of porpoises was observed--after lining up in a row, three of the animals quickly moved toward shore.

The Azov porpoises remained from a few dozen minutes to several hours in the hunting region, with their behavior and disappearance from this region being very difficult to record. As the result of several successful observations it was established that the hunting behavior among Azov porpoises alternated with the migrational. A group of dolphins would move for a long time in some direction and then suddenly cease this "purposeful" movement and begin to hunt. In the hunting region individual specimens could move "on their own." Then the animals would gather into a group again, which would swim away from the region of the observations.

Fewer individual behavior patterns were noted among the Azov porpoises than among the bottlenose dolphins. Two types of leaps were observed: a low horizontal leap and a "log" leap. Exposure of the tail and slapping the tail against the water were repeatedly observed. Noted twice was the turning over of the porpoise belly upwards, and once it seized a fish in this position. Leaps toward each other were noted among the group leaps (the animals usually leaped alternately).

On 5 August it was possible to observe in quite detailed manner the sexual behavior of the Azov porpoises in a group of three animals, one of which was a young porpoise with a "marking" (see above). The two adult dolphins often leaped out of the water, leaped over each other and swam for several seconds, with their abdomens pressed to each other (Fig. 19). The sexual behavior was observed for over 5 minutes. During this entire time the young porpoise swam first behind and then in front of the adults.

Common Dolphins

The migrational movement of a herd of belobochki [Delphinus delphis Linnaeus] white-sided dolphins was distinguished by its great swiftness.

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The animals moved at high speed, often leaping from the water. During the migrational passage the groups could be seen quite clearly--they as a rule consisted of 1-2-4 animals. In each group the dolphins would leap out in turn, one after the other. The hunting of white-sided dolphins was described in relatively great detail in the section on accompaniment in the catamaran. From time to time individual, slowly swimming white-sided dolphins were also seen in the biopolygon. This behavior was also, apparently, nutritive. In season II the similarity to the "carousel" and "boiler" was observed among the white-sided dolphins. The series of observations make it possible to assume the existence among white-sided dolphins of the "scout" phenomenon. On 21 August, near one of the bays, small groups of 2-4 animals were observed several hundred meters from the main herd. On 14 September 4 animals detached themselves from a herd of 25, behind the herd, they made a pass toward the shore and 3 minutes later again joined the herd. During this maneuver, the entire herd rarely slowed its movement and the diving of the animals became longer. The leaps of the white-sided dolphins, apparently, are similar in type to those of the bottlenose dolphins. We observed low horizontal leaps "like a log" and of "vertical climb." During the leap, however, the white-sided dolphins curved their bodies less than the bottlenose dolphins. The leaps of white-sided dolphins are described in detail in the article by Pilleri and Knuckey, 1967.

Therefore, a detailed analysis of several hundred situations in dolphin hunting makes it possible to reveal the great variety of the searching and hunting behavior of these animals. We singled out and described certain formerly unknown basic types of hunting behavior of dolphins in the natural habitat. These behavioral reactions of the search, detecting and catching of fish combine with each other and alternate during the hunt, depending on the type and number of the fish, the meteorological conditions, the presence of interference, and the number of dolphins taking part in the hunt. The abundance of procedures for hunting is impressive and, mainly, the great plasticity of the behavior of the dolphins, permitting them to react adequately to a change in circumstances.

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DESCRIPTION OF PULSED SIGNALS OF BOTTLENOSE DOLPHINS IN THE OPEN SEA

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[Article by V. M. Bel'kovich, V. V. Kaznadzey, S. A. Kreychi, E. A. Khakhalkina]

[Text] Among the numerous acoustic signals of dolphins, the majority are of a pulsed nature and are emitted in series of varying length and repetition frequency. The primary and principal biological function of pulsed signals is echolocation.

In an evaluation of the spectral characteristics of signals made by various researchers in the 1960's, broad use was made of a verbal description of them, while listening on the actual time scale, or with a delay. For example: a "bark" and "yelp" correspond to relatively short series of pulses with a repetition frequency of 400-500 pulses/sec. (Schevill, 1964); "squeak of door hinges"--to series with an increasing pulse repetition frequency 2-10 sec. long, etc. A more detailed classification of pulsed signals is also well known (Titov, Tomilin, 1970; Titov, Yurkevich, 1971; Markov et al., 1974), including that according to acoustic analogy: clicks--1-3 msec; resounding booms (4-9 msec); prolonged booms--up to 60 msec; crackling--from 100 to 1200 pulses/sec; quacks--series of pulses with the noise duty cycle in a range of 0.4-80 kHz, with a variable position of the energy peak in the range of 1.6-32 kHz and the length of the series 0.1-0.8 sec; bursts--series 30-180 msec long, with the noise spectrum of the pulse duty cycle in the range of 10-30 kHz; howl--with the length of the series 0.5-0.8 sec; a spectrum of the pulse duty cycle of 10-80 kHz with the energy peak within a range of 32-40 kHz; roar--a sharply increasing pulse frequency, and a wail--variable pulse frequency, changing according to a random law. Also displayed were complex signals, formed by imposing pulses on whistles, which is possibly related to the participation of the pulses in the structure of the messages during communication along with the whistle-like signals (Kaznadzey et al., 1975; Khakhalkina et al., 1977).

A great deal of attention was paid to the study of these questions by Vincent, R. G. Busnel, A. Dziedzic, D. Caldwell, M. Caldwell, J. Dreher, W. Schevill, W. Watkins, K. Norris and other researchers, references to

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which are contained in recent surveys (Dierks et al., 1973; Ayrapet'yants, Konstantinov, 1974; Bel'kovich, Dubrovskiy, 1976).

In the 1970's the researchers' attention was shifted strictly to the individual pulse. As a result, two opposing points of view were formed. According to one, the pulsed signals as a whole are quite stereotyped and standard, and according to the other--the pulsed signals are variable: the energy peak in the spectrum of pulsed series "floats," drawing on spectrograms structural (formant) bands of varying configuration (Schevill, 1964), the frequency in the series changes from pulse to pulse (Romanenko, 1964) and the peak of the spectrum, the pulse repetition frequency and duration vary to equal the task (Akopian et al., 1973; Ayrapet'yants, Konstantinov, 1972). All these data, however, were obtained under the conditions of a tank or pen. Therefore, the data on adaptation and variability of the pulses among dolphins in nature is of great practical interest. In performing bioacoustic research under the conditions of the open sea, we naturally attempted to gather and analyze material on the pulsed signals of dolphins under the conditions of their natural habitat.

Material and Method

We recorded the acoustic activity of the Black Sea bottlenose dolphin from May through September in the course of two (II and III) seasons, during observations of their behavior. The basic behavioral situation consisted of different stages of hunting fish by single dolphins and groups of 1, 2, 3 ... 12 dolphins in a biopolygon. Equipment with a passband of 0.1 - 100 kHz (Fig. 23) was used to record the signals. The recordings obtained were heard with an 8-fold lag, and analyzed on a 48-channel dynamic spectroanalyzer, described above.

Results and Discussion

In the auditory analysis of the pulsed signals, as well as the analysis of their spectral-temporal characteristics, obtained from the spectro-analyzer, it was noted that the classification of the pulsed signals by acoustic analogy, which was mentioned above, in general is retained, although within each type there are a number of variations in the pulsed signals, which can be clearly differentiated by ear (auditory) when transposed, and give rise to various auditory image representations. For example, Figure 30.1 shows the spectral-temporal characteristics of four series of pulsed signals, classified as clicks, which upon auditory analysis evoke the following associations:

a--the crack of a whip--short (3 msec), relatively infrequently spaced (115-145 msec) broadband pulses (0-80 kHz). More frequent pulses in the low-frequency area are noise interference;

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b--tapping a nail against glass--duration--3 msec, but the period of repetition is 20-25 msec and the energy peak is in the range of 18-80 kHz. On the spectrogram interference of a pulsed nature could also be seen, the source of which consists of mussels and shrimps (pulses of 10 msec and longer with a broad spectrum and energy peak in the low-frequency and high-frequency ranges);

c--rapping a rod against dry wood. Duration--3 msec, repetition period 15-20 msec, and they have a discontinuity in the duty cycle spectrum (the low-frequency part of the spectrum is 0-3 kHz; the high-frequency--12-80 kHz). Most of the energy is concentrated in the high-frequency area of the spectrum;

d--rolling sounds resembling pile-driving--a series of pulses with the repetition period up to 100 msec and the duration up to 3 msec in the low-frequency range and three times as long (up to 10 msec) in the high-frequency range (20-80 kHz).

Figure 30.2 shows the spectral-temporal characteristics of other pulsed signals, classified as booms. Characteristic of the entire group is a greater change in the time of the various sections of the spectrum than in the pulses shown in Figure 46.1, due to which the pulse on the spectrogram has the shape of a wedge with the point underneath. In an auditory analysis with transposition there are differentiated:

a--blows with a hammer along an iron plate--pulses 3 msec long in the low-frequency area of the spectrum and 15-20 msec in the high-frequency (spectrum up to 80 kHz), with the repetition period 20-50 msec;

b--gunshots--duration up to 30 msec in the high-frequency range of the spectrum (15-80 kHz) and 3 msec in the middle frequencies, with the repetition frequency 95-115 msec. Present at the same time is interference from shrimps in the form of chaotic crackling in the high-frequency range;

c--bursts--duration up to 60 msec, spectrum--18-80 kHz. The great intensiveness and high percentage of encounter rate in hunting situations permit the assumption to be made that they are used to deafen the fish;

d--rumbling of a tractor motor, alternating with discharges from an exhaust pipe. A series of location pulses increasing in frequency, which indicates the dolphin's coming close to the target (Norris, Turner, 1967; Bel'kovich, Reznikov, 1971) and usually ends with a "quack" or "roar" characteristic when catching the fish.

As was already noted above, the pulsed signals are emitted by the dolphins usually in series, which are distinguished by the duration, as well as by the mutual spacing of the pulses within the series. For example, for

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series classified as crackling a duration of up to several seconds is characteristic, with the length of each of the pulses being 1-3 msec, the pulse repetition frequency 5-15 msec and the change according to a random law of the spectral density during the series, which from the auditory standpoint makes them similar to the operating sounds of various mechanisms and machines. Figure 30.3 shows certain characteristic cracklings which, when transposed 8-fold, can be easily distinguished by acoustic analogies:

a--a circular saw--pulses with the repetition period about 8 msec, and have a broad "slump" in the spectrum in the middle frequencies, which by the end of the series narrows down and disappears;

b--a tractor moving along where there is no road. The energy of the pulses is concentrated in the high-frequency range (18-80 kHz) and the repetition period of the pulses changes sharply from 15 to 2 msec;

c--motorcycles picking up speed. The repetition frequency varies from 20 msec to 5 msec. The basic energy of the pulses is concentrated in the low-frequency and high-frequency ranges of the spectrum, while in the middle frequency ranges the spectrum changes according to a random law;

d--a short machine-gun burst. The pulse repetition period decreases from 5 msec to 1 msec, at the beginning of the series the energy peak is concentrated in the high-frequency range, and by the end expands sharply.

All the time intervals and frequency values of the spectral components analyzed above the pulsed signals are given on an actual scale, while the description using the auditory analogy of individual pulses and their series was made with an 8-fold lag. Therefore, the relative scale of all types of signals is retained. It must be remembered, however, that on the real time scale all the pulsed signals are distinguished for us only by the repetition frequency. For example, Figure 30.4 shows the spectrograms of the sounds of the dolphins perceived by the ear as a "roar" (a), "wail" (b) and "quack" or "mew" (c). These sounds are a series of short pulses (1-3 msec) with a relatively uniform density of the spectrum of 0-80 kHz and very short interpulse interval (pulse repetition frequency from 500 to 1200 pulses/sec). As a rule these sounds conclude the locating when catching the fish.

Here it should be said that the frequency boundaries of the energy distribution in the spectrum of these series may be modulated, describing a certain contour, similarly to the envelope of the time-frequency characteristics of the basic tone of the whistle-like signals.

When analyzing the sounds of a pair of dolphins in a tank, we also recorded the series of pulsed signals, the spectrum of which was concentrated in a

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relatively narrow band of frequencies and was modulated so as to describe a certain contour, analogous to the contour of the envelope of the whistle-like signals (Figs. 31, 32). These changes in the spectrum in the series of pulsed signals, upon comparison with the behavior at the moment of emission, then permitted the assumption of the possibility of their use in communication (Kaznadzey et al., 1976; Khakhalkina et al., 1975), and the spectral-temporal analysis revealed certain special features that indicate the possibility of arbitrary control of their spectral-temporal structure (Fig. 31) by means of several simultaneously operating sources, as well as resonators rearranging the structure of the signals.

The above comparisons of objective spectral-temporal characteristics and subjective auditory analysis of the pulsed signals of dolphins, when transposed, show that man can easily distinguish subtle changes in the spectrum, duration and repetition frequency of these signals. This permits the assumption that the dolphin also differentiates the above-noted changes in the parameters of the "stereotype" pulses, since the dolphins' acoustic analyzer possesses a higher resolving capacity for the procedure (Vel'min, Dubrovskiy, 1975; Bel'kovich, Dubrovskiy, 1976) and it is possible that this is used as an additional source of information.

One must, however, take into consideration the fact that there is still a great deal that is unclear with respect to the question of the variability in the structure of the pulsed signal. As was noted above, some people feel that the dolphins' sounding pulses are always stereotyped, and the variations in the spectral-temporal characteristics recorded are brought about by a change in the dolphin's directivity diagram, due to turning the head. Others think it is possible that there is arbitrary control of the spectral-temporal characteristics of the pulses, on the basis of the series recorded in the situation of the animal's fine adjustment to the conditions of the experiment (see the surveys, Ayrapet'yants, Konstantinov, 1974; Dubrovskiy, 1975). Probably, the truth lies somewhere between, namely, depending on the situation and the conditions of the study of the sounding signals, the dolphin uses the discontinuity of its pattern for sufficiently fine tuning (Bel'kovich, Dubrovskiy, 1976). If this does prove to be efficient for recognition, the other animals may receive quite a large amount of additional information on both the target and the source. On the other hand, the reason for the change in the signals with respect to duration and position of the energy peaks in the spectrum in the pulse series may be related merely to the biological nature of the transmitter, which for some reason is forgotten about and which ensures both a certain stability in the parameters of the pulsed signals and a certain dispersion of them. The above-noted characteristics of the pulsation are apparently inherent in the transmitter of each animal, and this individuality is undoubtedly important for recognition of individuals, and for orientation, determining the mutual positioning, etc. This biological instability of each transmitter may prove to be

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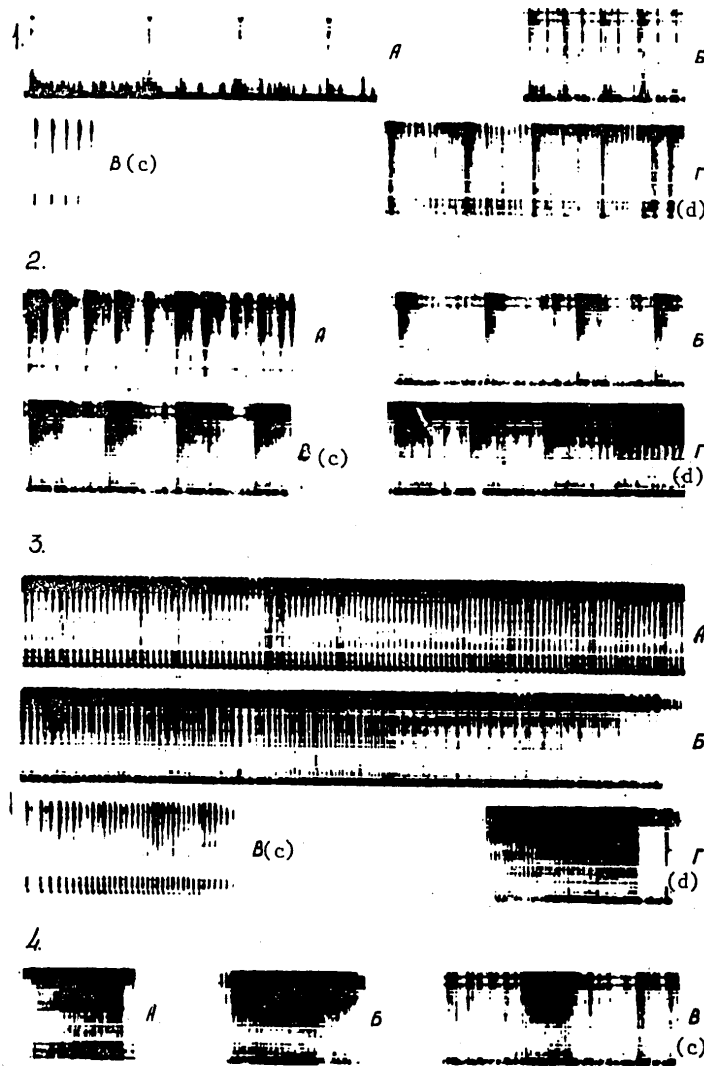


Figure 30. Spectrograms of the Basic Types of Pulsed Signals of Dolphins in Nature

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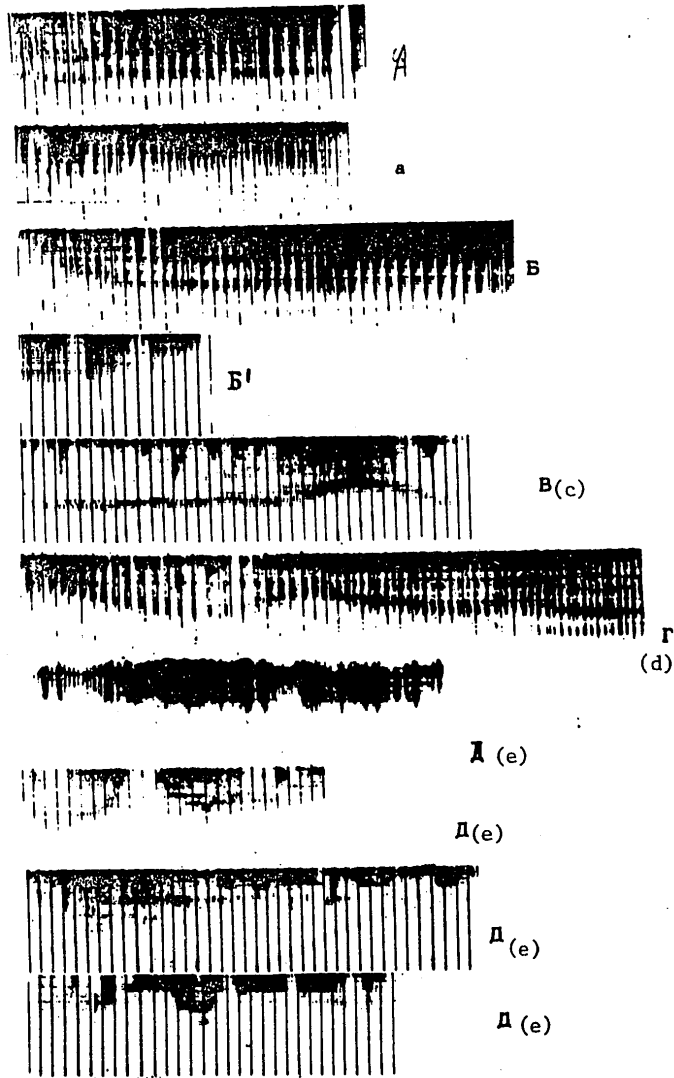


Figure 31. Spectrograms of Pulsed Signals of Dolphins Under Conditions of Captivity

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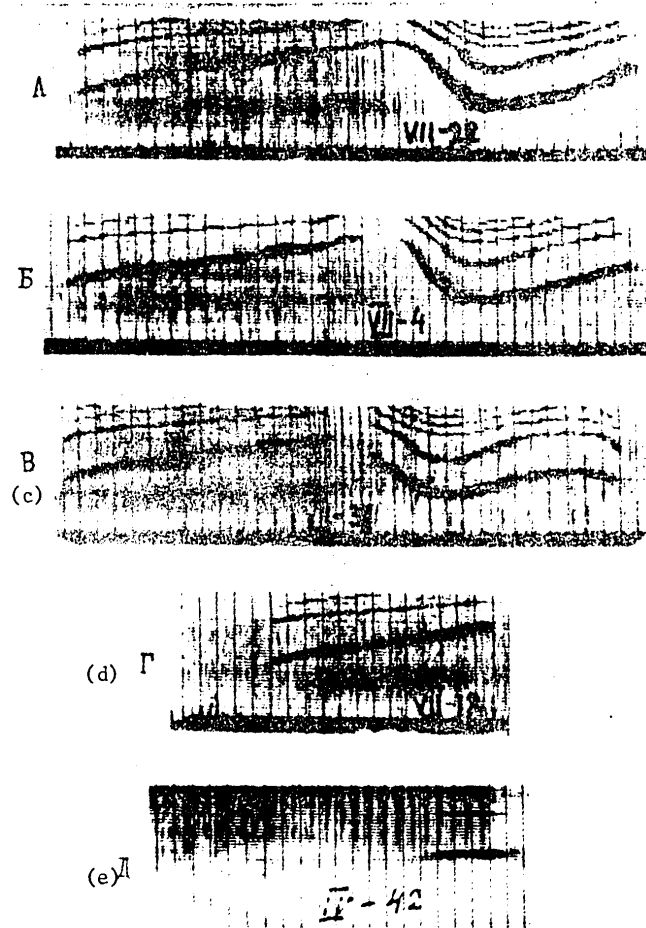


Figure 32. Spectrograms of Pulsed-Whistle Signals*

*It is assumed that the whistle signal bears an emotional or individual-recognition load, while the pulsed component serves to establish the address channel of communications for directed transmission of any whistle signal.

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no less important for the locational perception of the targets as well, since above all, it eliminates fatigue and the nervous centers' habituation to uniform echosignals (Bel'kovich, 1972).

When using acoustic pulses, the dolphin is forced to tune out the pulsed interference that is constantly present under natural conditions. The spectrograms shown above are "cluttered" with the noise of surf, the sounds of mussels, shrimps, etc., which have a constant spectrum in time. This constancy of the spectrum is obviously one of the reliable criteria for singling out the signal, because the difference in the spectrums and the modulated nature of the dolphins' sounding signals make it possible to distinguish them easily from the interference.

It is thought that the principal and primary biological function of the pulsed signals is echolocation, which ensures the dolphins' orientation in the aquatic environment, where its visual analysis is excluded at great distances, but considerable possibilities are afforded for the development and use of an acoustic system of monitoring (evaluation and analysis) of the environmental habitat and, accordingly, adequate organization of behavior in it (Bel'kovich, 1972, 1974). The dolphins' echolocation (acoustic) analyzer may serve as an example of the adaptive development of this system for acoustic analysis of the environment and its use in organizing behavior.

It is expedient to show the given functional-ethological specificity of various types of series of pulsed signals in relation to certain situations and the nature of the dolphins' behavior. For example, series of pulsed signals are used for orientation during migrations and when maneuvering during a search for fish. Most often they are related to the detection of the catch, but particularly with its pursuit during the hunt. In this case an increase in the frequency of the transmission of pulses indicates that the dolphin has begun active pursuit of the catch (Bel'kovich, Reznikov, 1971), which is usually noted only from a distance of about 0.5-0.3 meters (Fig. 30.2g). This increase in the pulsation is usually completed at $1/f \sim 250-800$ pulses/sec, which is perceived by our ear as a roar ("mewing" or "quack"), which is emitted at the moment of seizing the catch. Sometimes this echolocation series, with acceleration of the pulse repetition does not end with a roar, which indicates that the dolphin has missed the catch. Therefore, one may calculate the number of fish eaten during the course of the hunt by the number of roars.

Uniformity and slowing down in the pulse repetition frequency in the series (5-30 pulses/sec) corresponds to the orientation of the dolphins and the scanning direction finding (of the fish) in the initial phases of the hunt. Individual clicks are usually also used by dolphins as a duty practice, and ensure orientation and search of fish. Booms are distinguished by greater power (width of the spectrum) and a relatively long duration (up to 60 msec). The functional significance of the booms is not yet completely clear, but in consideration of their physical

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characteristics and the use mainly during active devouring of the fish by a group of dolphins (64.2%) (Table 7), it may be assumed that they are used to disorient and deafen the fish during the hunt.

Conclusion

The auditory analysis made showed that the pulsed signals used by the dolphins occur during transposition of the characteristic sound image representations, which are easily memorized and clearly recognized by the operator. It is possible that due to this, they may play a certain informative role for a group of dolphins as well, by creating an acoustic picture of a behavioral situation as a whole and the action of each of the members of the group individually.

In an auditory analysis with transposition of the acoustic circumstances (context) in various behavioral situations, it was also noted that a combination of different sounds creates fully definite sound images (pictures) of the situation: "construction," "individual shooting," "air combat," "motorcycle races," etc. A set of such sound pictures obviously is also limited, just as a set of types of group behavior. This makes it possible, from the acoustic circumstances (picture), to recreate in the first approximation the behavioral pictures of what is taking place in the water, and to compare them with visual ethological observations. This comprehensive ethological-acoustic approach was used for the first time.

There is no need to prove that such information can be useful in organizing group actions of dolphins under conditions of the natural habitat, particularly since our observations of the dolphins' behavior indicate a high level of interaction and organization in the behavior of dolphins in a group.

The abundant representation of pulsed signals in the situations (about 90% of all the signals) gives reason to assume that in the process of the evolution of dolphins' communicative system, the informative surplus of pulsed signals began to be used by the dolphins for communicative purposes, in combination with the whistle-like signals. This signaling could contribute to more efficient intragroup organization and to the development of the complex forms of behavior which we observe.

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CHARACTERISTICS OF THE DOLPHIN' SONAR FUNCTION

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[Article by Ivanenko, Yu. V., Ivanov, M. P., Nonin, Yu. A., Chilingiris, V. I.]

[Text] This article gives a brief survey of our studies of the sonar system of the Black Sea Bottlenose Dolphin (*Tursiops truncatus*), and also formulates a number of hypotheses on the possible principles of the functioning of certain elements of this system.

1. As a locational click, the dolphin primarily uses one- or one-and-a-half phase pulses with a duration of 7-100 msec, with a pulse duty factor somewhat greater than twice the time for transmission of the signal to the object of location (Ivanenko, Ivanov, Telekhov, 1977).

All the existing physical models of the generation of location pulses of the dolphin cannot explain the existence of the brief (tenths of a msec) signals of a nonresonant nature, which we have recorded in various experiments with the animals. To solve this problem we advanced the hypothesis of the compression of the frequency modulation of the dolphin's signals in the frontal protuberance (Nonin, 1977).

2. An analysis of histological specimens of the frontal protuberance revealed the complexity and nonuniformity of its structure (Bel'kovich, Nesterenko, 1971; Agarkov, Khomenko, Khadzhinskiy, 1974).

We will discuss the frontal protuberance of the dolphin, which consists of connective tissue and individual fat cells, as a two-component water-like medium with varying values of density and compressibility. By medium we will mean the connective tissue, and by micro-nonuniformities--the fat cells.

When studying arbitrary, including wave, motions of the continuums, the initial system of equations consists of Euler equations, valid for the ideal medium. In a one-dimensional case we have:

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$$\frac{\partial \rho}{\partial t} + \frac{\partial}{\partial x} \rho v = 0, \quad (1)$$

$$\frac{\partial v}{\partial t} + v \frac{\partial v}{\partial x} = -\frac{1}{\rho} \frac{\partial P}{\partial x}, \quad (2)$$

$$P = P(\rho), \quad (3)$$

where ρ is the density of the mixture of the two components, P is the pressure and v is the velocity of the particles of the medium.

This system is complete and consists of a continuity equation (1), an equation of motion (2) and an equation of state (3).

Passing through the frontal protuberance, the wave of pressure causes a pulsation of the fat cells. Therefore, in the nonuniform medium under discussion, Euler's equations should be supplemented with an equation for the small oscillations of the cell. The movement of the surface of the compressed cell may be described by Rayleigh's equation:

$$R\ddot{R} + 3/2\dot{R}^2 = \frac{1}{\rho_0}(P_1 - P_0), \quad (4)$$

where R is the radius of the cell, ρ_0 is the density of the medium, P_1 is the pressure inside the cell, P_0 -- the pressure in the medium. The derivatives for time are designated by the points.

When solving the system of equations (1) - (4) jointly, we arrive at a variance ratio linking the speed of sound (C) in the two-component model of the frontal protuberance of the dolphin under discussion with the frequency of the oscillations being transmitted (ω) and the relative concentration of the fat cells (nV_0):

$$C^2 = C_0^2 (1 - nV_0)^2 \frac{\left(1 - \frac{\omega^2}{\omega_0^2}\right)}{\left(1 - \frac{\omega^2}{\omega_0^2}\right) + nV_0}. \quad (5)$$

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Here C_0 is the speed of sound in the tissue in the absence of fat cells ($nV_0 = 0$); ω_0 is the resonance frequency of the cell, which according to our estimates is a value in the order of 350-420 kHz.

From the ratio (5) it follows that with an increase in the concentration of the fat cells (nV_0), the speed of sound will decrease ($C \rightarrow 0$); an analogous phenomenon will be observed when $\omega \rightarrow \omega_0$. The first fact indicates that in the dolphin's frontal protuberance there should be a spatial dispersion of sound connected with the nonuniformity of its structure, and the second--that there is a frequency dispersion, with the high-frequency harmonics being propagated more slowly than the low-frequency. The possibility of the dolphin's fatty cushion functioning as a nonuniform coated retarding lens has been noted in works (Bel'kovich, Nesterenko, 1971; Nesterenko, Rezvov, 1973). A mathematical examination of the acoustic properties of the dolphin's frontal protuberance reveals a possible physical mechanism of an influence, through the nonuniformity of the fatty cushion, on the passing sound wave, which lies in the nonlinear and dispersional nature of the interaction of the wave and the fat cells (Nonin, 1977).

Model experiments to determine the speed of sound in specimens taken from various areas of the fatty cushion of the dolphin have shown that the speed of sound in the center of the frontal protuberance is approximately 10% less than in the peripheral area (Norris, Harvey, 1974). In these experiments, however, it was assumed a fortiori that the speed of sound would not depend on the frequency and length of the transmission path of the acoustic signal. Otherwise, the results should be different.

As was noted above, the existing physical models of the generation of the locational signal of the dolphin are unsatisfactory. Therefore, we made an experimental attempt to ascertain the possibility of compression of the frequency modulation of the signal in the frontal protuberance. The experiment was conducted in a sound-anechoic tank measuring 290 X 60 X 50 cm, filled with sea water. The measured reflection factor of the acoustic rubber used to deaden the sound did not exceed 0.1 in a frequency range of 10-200 kHz.

The dolphin's head was rigidly fixed so that the distance from the emitter introduced through the blow hole to the area of the tubular sacs up to the surface of the water was 20-25 cm. The pickup hydrophone was placed 15-20 cm from the tip of the rostrum on its axis.

Used as the oscillator was a sphere \varnothing 10 mm made from TsTS-19 piezoceramic, calibrated for the emission, and as the pickup hydroplane--a sphere \varnothing 7 mm made of the same material.

The signal generator was a specially designed pulse frequency modulation generator with the following parameters: ranges of change in the carrier

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frequency (f_H) 30-130 kHz; change in the deviation (D) from the value of the carrier by 0-60 kHz according to the falling law, the duration of the pulses could vary within the limits of 0.1-10 msec, the repetition frequency--from 2 to 250 $\frac{\text{pulses}}{\text{sec}}$, and the nonlinearity of the output signal, less than 3%.

The nonuniformity of the amplitude-frequency characteristic of the entire receiving-transmitting channel did not exceed 3 dB.

Figure 33 shows the results of the experiment, with the following values of the parameters of the signal emitted: duration of the pulse 1 msec, repetition frequency 40 Hz, $f_H = 120$ kHz (Fig. 33 A). It turned out that with the introduction of a negative frequency modulation, the signal being transmitted, in passing through the frontal protuberance, breaks up into two groups of pulses, and, with an increase in the deviation, the duration of the groups themselves, as well as the components of the group of pulses, decreases (Fig. 33 d-e). This fact may be interpreted as a compression of the emitted signal and--confirmation of the theoretical conclusions as to the existence in the frontal protuberance of frequency dispersion.

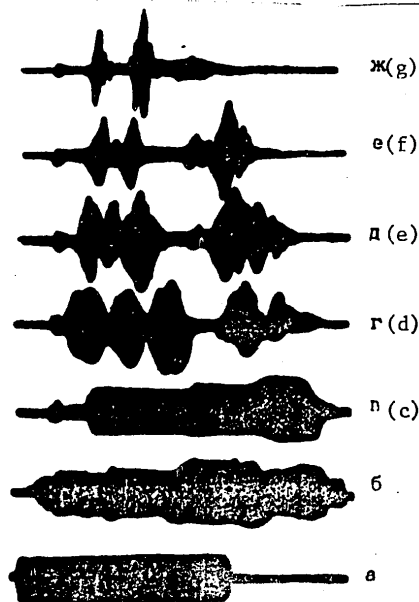


Figure 33. Change in the Structure of Signals Passing Through the Frontal Protuberance, Depending on the Deviation (Δ) of the Frequency in kHz

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It should be noted that the results of the experiment depended on the degree of freshness of the specimens. (The experiment was conducted at a different time on three heads of bottlenose dolphins). After the head had been in the refrigerator (at -3°C) for a certain time, the amplitude of the signal transmitted dropped, the compression disappeared and reverberation interference began to appear (defocusing occurred). Analogous changes were also observed at the end of the experiment, if it lasted long enough. These facts also indicate that the mechanism of interaction of the sound field with the tissues of the frontal protuberance cannot be explained merely from the standpoint of the nonuniformity of its structure (different average density). The theoretical model suggested by us, even though it may qualitatively explain the results of the experiment, for a quantitative comparison requires detailed study of the physical properties of the dolphin's fatty cushion.

3. In the behavioral experiments, conducted according to conditioned reflex methodology, using multichannel recording of the sounding signals (Ivanenko, Ivanov, Telekhov, 1977), we studied the characteristics of the directivity of the acoustic field of the dolphin during emission. The results of the experiment showed that the width of the characteristics of directivity for a level of 0.7, calculated according to the envelope of the pulses, is 14° on the horizontal plane and 7° on the vertical (Fig. 34). The coefficient of concentration of the acoustic power is 550.

Along with the high directional properties, the dolphin's transmitting system makes it possible to form acoustic pulses, the temporal structure of which depends on the direction of the propagation in space. If the shortest and broadest-band signals (with the spectrum peak in the range of 60-90 kHz) are transmitted in the direction of the rostrum (acoustic axis), then with a deviation from the acoustic axis, the duration of the signals increases, and their spectrum, accordingly, is reduced in the area of the lower frequencies.

A harmonic analysis of the integrated beam pattern, made on a BESM-6 electronic computer, revealed that the nature of the formation of the sound field for low and high frequencies was different in principle. If, for the components of the spectrum in a range of 10-50 kHz, the directivity is of a clearly marked double-lobe nature, with the minimum in the direction of the acoustic axis up to $(-10 \div -14)$ db, then in the area of frequencies of $70 \div 120$ kHz a narrow emission is observed. This fact makes it possible to explain the changes in the spectral and temporal characteristics of the signals which are observed when they are recorded from different directions (Ivanenko, Ivanov, Telekhov, 1977).

4. In the overall range of problems facing researchers of the dolphin's echolocation system, a central place is occupied by the problem of the animals' discrimination of the acoustic images, as well as by the problem of adaptation to a certain specific locational situation.

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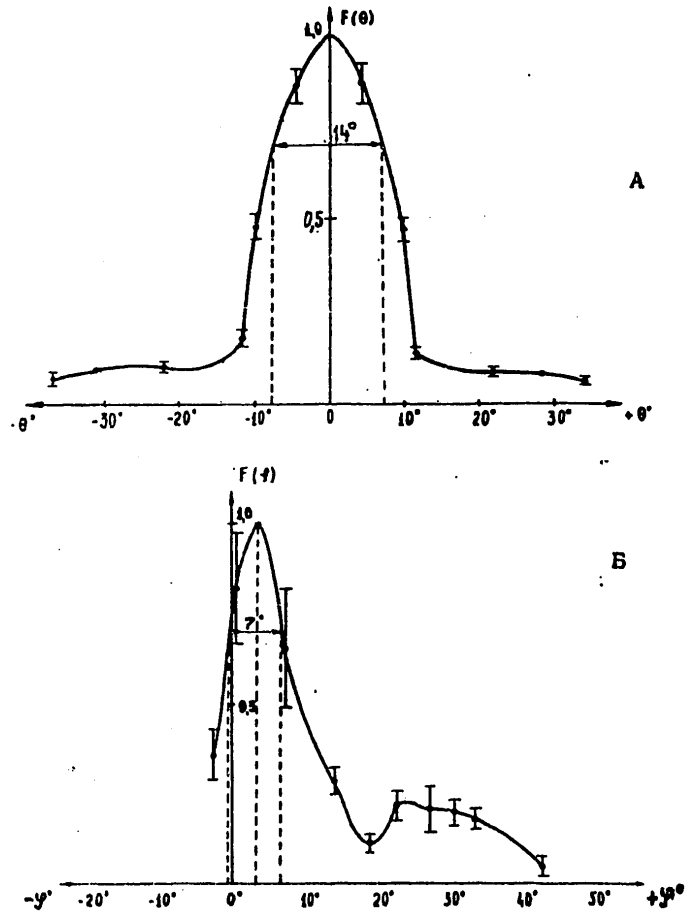


Figure 34. Diagram of the Directivity for the Emission. A--on the horizontal, B--on the vertical plane

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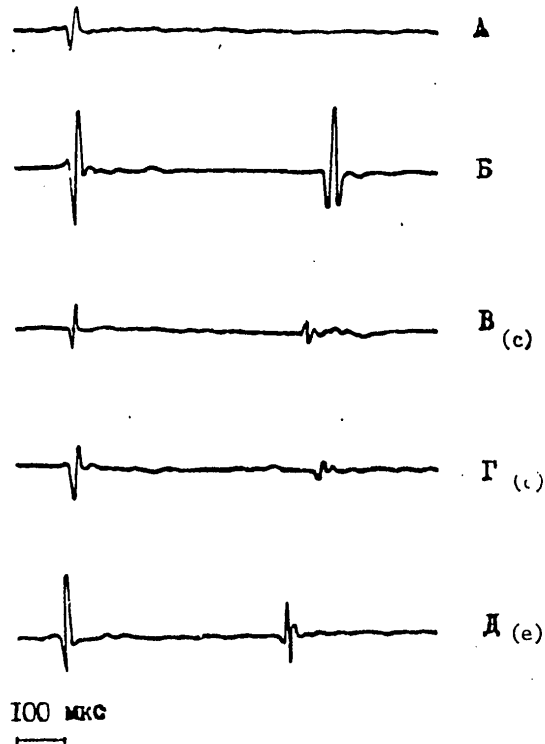


Figure 35. Oscillograms of the Sounding (at the left) and Echo Signals of Bottlenose Dolphins. A--in absence of targets. B--duraluminum plate 10 mm thick. C--duraluminum plate--1 mm. D--steel sphere b 100 mm. E--duraluminum cylinder $h = b = 100$ mm.

From the results of the works published, it follows that bottlenose dolphins are capable of differentiating metal plates made from both the same and different materials, even if the intensities of the signals reflected, estimated according to Rayleigh's well-known formula, are identical for the pair of plates presented in the experiment (Evans, Powell, 1967; Evans, 1973).

In experiments on recognition and ascertaining the adaptational potentials of the dolphin's sonar, we recorded both the probing signals and those reflected from the targets offered. Figure 35 shows the pulses emitted

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by the dolphin and the signals corresponding to them, reflected from various objects.

In experiments to differentiate duraluminum plates 1.3 and 10 mm thick, we obtained data on the change in the duration of the sounding pulses. Statistical processing of the results showed that the dolphin, located at the starting position, in the absence of the target emitted locational pulses, the main proportion of which consisted of clicks lasting 20 msec; when a positive target was presented (10 mm), signals lasting 15 msec predominated, and with the correct differentiation of the negative target (3 mm) signals lasting 10 msec predominated in the pulse series.

The signal reflected from the plate 1 mm thick arrived inverted with respect to the phase, and the dolphin differentiated it from the first presentation. It should be noted that this task was not a threshold task for the animal, but nevertheless the question is interesting: why does the dolphin shorten the signal with increased complication of the locational circumstance. For this purpose we discussed theoretically the question of the reflection of the pulse in the form of a scrap of a sinusoid of a thin indefinite metal plate.

The problem was solved by the method of summing up the train of signals rereflected by the front and back planes of the plate. By omitting the intermediate computations, we will present here the definitive type of formulas used in the calculations.

In the period of time $0 < t < T$ for the shape of the reflected pulse, we have:

$$f(t) = A_{12} \sin \omega_0 t - B_{12} \cdot B_{21} \sum_{n=1}^{\infty} E\left(\frac{t-T_0}{T_0}\right)^{2n-1} A_{12} \sin \omega_0 (t-nT_0) \quad (6)$$

After transmission of the basic pulse, for the time $t > T$, the shape of the pulse will be defined by the expression:

$$f(t) = B_{12} \cdot B_{21} \sum_{n=1}^{\infty} E\left(\frac{t-T}{T_0}\right)^{2n-1} A_{21} \sin \omega_0 (t-nT_0) \cdot E\left(\frac{t-T_0}{T_0}\right) \quad (7)$$

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The following designations are introduced here: A_{12} -- the reflection factor from the boundary of water-metal; B_{12} -- the transmission factor; A_{21} -- the reflection factor from the boundary of metal-water; B_{21} -- the transmission factor; T -- the length of the pulse; T_0 -- the doubled time of transmission of the pulse through the plate; $n = 1, 2, 3, \dots$; ω_0 -- the frequency duty factor; E -- designates the integral part of the number.

Figure 36 shows the pulse, computed according to formulas (6) and (7) on a Promin' electronic computer. An analysis of the expressions given here permits the following conclusions to be drawn: 1. A change in amplitude of the echo signal and its duration will be more greatly marked, the smaller the ratio $\frac{T}{T_0}$. 2. The echo signal always has an additional half-cycle, the duration of which is approximately equal to $5 T_0$. 3. The shape of the transmitter pulse and the number of intervals in it in principle do not affect the nature of the conformities to principle of 1 and 2.

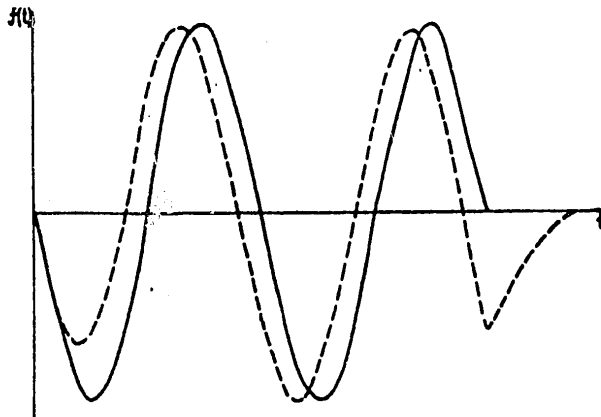


Figure 36. Shape of the Pulse Reflected From a Duraluminum Plate 10 mm Thick (dotted line). The Solid Line Shows the Probing Signal, 60 msec Long.

It should be noted that the plates 1 mm thick and less may act as absolutely compliant boundaries and implement the turn-over of the phase of the reflected signal (Fig. 35 c).

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Therefore, the effect observed in the experiment of the adaptive shortening of the transmitter pulses, with the complication of the locational task in the case of the plates has a fully satisfactory explanation.

5. The question of the maximum distance at which the dolphin can detect the targets is an interesting one. In an experiment which was made using the method of the motor-food conditioned reflexes, the dolphin was located in a pen, and the targets were presented to it from a boat that was moving alongside a cable stretched out to a distance of up to 150 meters from the place where the animal was located. Within the limits of this distance we recorded the presentation of the targets with an error not exceeding ± 1 meter. In the net separating the pen from the sea a gate was made, at the lower edge of which a perforated pipe passed. At the moment when the boat moved alongside the cable and when the target was lowered into the water, compressed air was fed into the pipe and the curtain of bubbles made it impossible for the dolphin to "make a decision" on the presence of the target on the basis of circumstantial factors.

In the experiments maximum distances were consistently found for the dolphin's detection of steel balls, from 10 to 100 mm in diameter. The value of the diameters of the spheres changed every 10 mm. Statistical processing of the results showed that the maximum distance from which the dolphin detected the 10-mm sphere was 10 m, and the ball 100 mm in diameter--120 m from the animal's starting point.

In the process of prolonged training (the experiment lasted 1 month and on the average each target was presented to the animal 70 times), the distances from which the dolphin detected the balls with 90%-probability increased in the initial experiments and then stabilized. In the control experiments, when the animal was presented all the targets (from 10 to 100 mm) consecutively in the same experiment, the amplitude of the signals could change 10-fold with the locating of any target at the threshold distance. No regular increase in the intensiveness of the probing signals with an increase in the distance to the targets (and, correspondingly, in their diameters) was observed in the dolphin being trained.

A comparison of the experimental curve of detection with the angular dimensions of the targets presented showed that for the dolphin there is a minimum angular threshold dimension for the ball with a diameter of 50 mm at a distance of 80 m. Theoretically this distance is optimum for the sonar, operating in a frequency range of 100-120 kHz. According to our data, this figure also corresponds to the area of maximum hearing sensitivity in bottlenose dolphins.

It should be noted that, even though the nature of the sound field reflected from the spheres is related to their modulus of the scattering range, the effect of the latter on the reflection of a short wideband pulse will be little.

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Therefore, the conclusion may be drawn that for a dolphin, under the conditions of the natural habitat, there exists an optimal detection distance, related to the conditions of the propagation of the signal in the water, energy expenditures for emission and the ecological characteristics of the species. An adequate condition for life in an aquatic environment, this distance should not essentially depend on the properties of the object of location; in our experiments it was a value of 80 m.

On the basis of the threshold auditory sensitivity of the dolphin, determined in the experiments, the energy parameters of its location signals, the spatial characteristics for the emission and the laws of propagation of sound in water, we estimated the maximum possible distance for the animal's detection of a perfectly reflecting target, which was a value in the order of 1.5 kilometers.

6. Dolphins' use, under echolocation conditions, of short, broadband pulses, greatly differing in duration from the signals of land locating animals, implies a specific organization of the functions of their auditory system. This particularly pertains to the level of its sensitivity to the range of frequencies that is most informative in the dolphins' signals. According to data obtained on six animals, the range of maximum auditory sensitivity to long tonal samples falls in frequencies of 40-130 kHz. In this range the animals perceived signals with an intensity in the order of 10^{-16} - 5 and 10^{-17} w/cm². In the direction of the lower and higher frequencies, the thresholds of perception increase monotonally to 0.3-0.5 and 0.8 dB/kHz.

Along with the frequency discrimination, a necessary condition for an efficient spatial analysis is localization of the source of the sound. We therefore concentrated our attention on the directional sensitivity of the dolphin's acoustic analyzer under conditions corresponding to passive location.

In our experiments, the parameters of the pattern of directivity of the bottlenose dolphin's acoustic system were determined according to the values of threshold sensitivity to tonal and pulse signals coming to the animal at different angles on horizontal and vertical planes.

Measurements of the threshold sensitivity on the horizontal plane with a successive change of position of the transmitter to various points in the pen (eight points) showed that the minimum thresholds for tonal samples of frequencies of 30, 50, 80 and 120 kHz were observed when the signals were presented in front of the animal's rostrum (Ivanenko, Chilingiris, 1973). In subsequent experiments we studied signals from 34 points, which made possible a more detailed evaluation of the bottlenose dolphin's directional sensitivity. Figure 37 shows the patterns of directivity of the acoustic system on the horizontal plane, plotted according to the mean values of the threshold magnitudes. Statistical processing of the

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data showed that all the patterns could be considered as symmetrical in relation to the acoustic axis, and the deviations observed did not go beyond the limits of the spreads of threshold values, which in these experiments were ± 3 db. For a frequency of 30 kHz, the width of the pattern of directivity is $40^\circ \pm 10^\circ$, and for 120 kHz, the pattern narrows to $10^\circ \pm 3^\circ$ at a level of 0.7. When the transmitter was placed opposite the acoustic meatus, (on the diagram this corresponds to 90° and 270°), the lowest drop in sensitivity as compared with the zero direction was noted for a tone of 30 kHz and was 3-7 db, and for the rest of the frequencies the thresholds rose by 20-26 db. The sensitivity of the dolphin's hearing for all tonal samples transmitted in the sector of angles of 90 - 270° was identical.

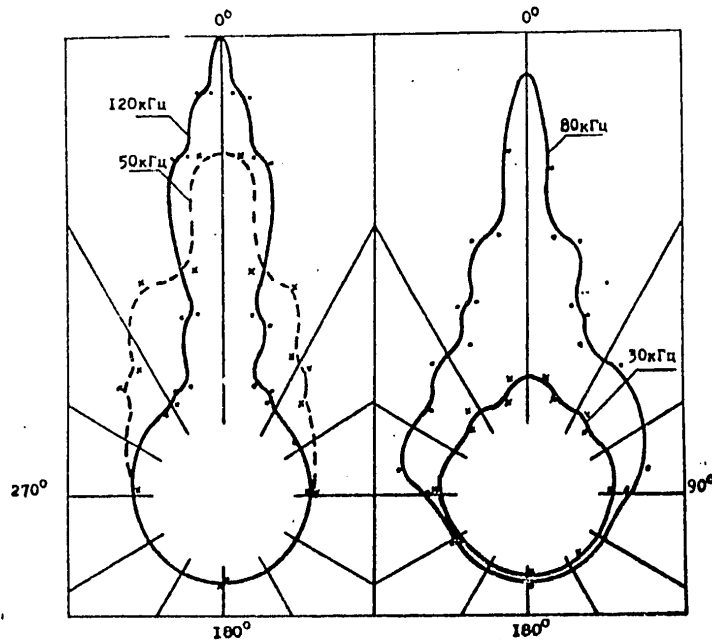


Figure 37. Pattern of Directivity of Reception of a Bottlenose Dolphin of Monofrequency Signals (Horizontal Plane). The Relative Values of the Directional Sensitivity Are Placed Along the Radii. The Absolute Threshold for a Tone of 120 kHz Was Taken As a Unit.

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The existence of drops in the threshold sensitivity (to 5 db) when the transmitter was shifted by 2° - 10° was characteristic of the pattern of directivity of receiving the tonal signals. The number of drops is not identical for signals of different frequencies. For example, for a tone of 30 kHz their number was three, for 50 kHz--four; and for 80 and 120 kHz--six drops in sensitivity.

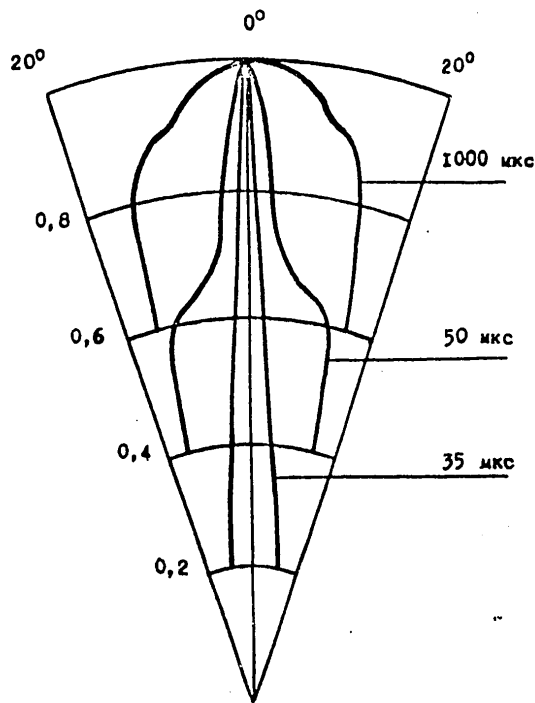


Figure 38. Pattern of Directional Reception of Pulsed Signals With Frequency of Duty Cycle = 30 kHz

We were forced to limit the estimate of the beam pattern on the vertical plane to a study of the threshold sensitivity of the dolphins' hearing to sounds coming from below. Measurements of the directional sensitivity showed that the maximum sensitivity for signals of all frequencies in the sector of angles studied was observed when the signal was presented

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directly in front of the animal, on the continuation of the axis of its body. The width of half the beam pattern was--for 30 kHz-- $13^{\circ} \pm 4^{\circ}$, for 50 kHz-- $4^{\circ} \pm 2^{\circ}$ and for 80 and 120 kHz-- 1° . The absolute sensitivity to signals from directions of over 40° becomes constant up to 180° , and the differences observed are contained in the value of the root-mean-square deviation from the mean value.

The relationship noted between the sharpening of the directivity of receiving the tonal signal and the increase in its frequency made it possible to assume that with a reduction in the duration of the sound stimulus and, accordingly, with an expansion of its spectrum, a tendency toward a change in the pattern should be observed. With an increase in the length of the pulse, when the principal energy is concentrated near the carrier frequency, the beam pattern should approach this for a monofrequency signal. The experiment confirmed this assumption (Fig. 38).

The characteristics of the directional receiving of the pulsed signals may be explained, on the one hand, by the heightened sensitivity of the acoustic analyzer to high-frequency components of the spectrum, and on the other hand--by the filtering properties of the sonar receiving system.

7. In this connection there should be a more detailed discussion of the evaluation of the dolphin's hearing properties, as a receiving system in which spatial-frequency filtration of the locating signals may be implemented. We will discuss the directional pattern of the receiving in accordance with the frequency-threshold curve of the acoustic analyzer, i.e., we will evaluate the spatial hearing as a function of three values --the threshold sensitivity (P), the direction of the arrival of the signal (θ) and the frequency (f).

A certain specific amplitude-frequency characteristic of the receiving channel (filter) corresponds to each direction for the source of the signal. The characteristics of these filters (on the horizontal plane) are shown in Figure 39, where the dotted line designates the conditional shape of the curves, in accordance with an increase in the thresholds in a range of frequencies below 30 kHz and above 120 kHz. We will observe an analogous picture if we examine the characteristics of filters on the vertical plane. From this the conclusion should follow that when the dolphin scans with its head in space, the signal may be consecutively passed through filters with a different amplitude-frequency relationship.

From the theory of communications, it is known that to construct an optimum filter, singling out the signal against a background of noise, a circuit must be synthesized, the transmitting function of which would be completely tracked with the spectrum of the signal being received (correct within the factor and the delay).

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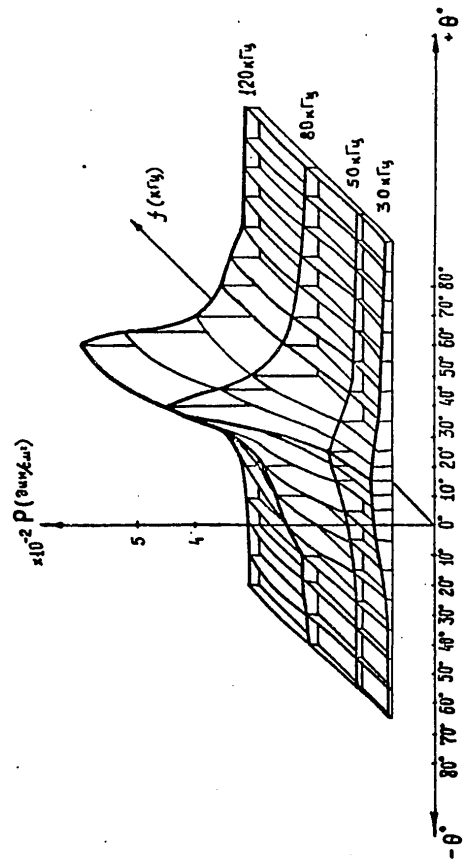


Figure 39. Spatial Characteristics of the Directed Reception on the Horizontal Plane

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If one turns, for example, to the characteristics of a filter corresponding to signals coming from the direction 0 (Fig. 40), attention is drawn by the fact that in their shape they almost repeat the envelope of signals transmitted along the rostrum (Ivanenko, Ivanov, Telekhov, 1977). Consequently, the dolphin's receiving system is always matched to its own transmitter pulses, transmitted in the direction of maximum concentration of the acoustic power, which considerably surpasses the efficiency of sonar during detection. In this there can be traced a clearly marked correlation of functionally different units of the dolphin's locator-transmitting and receiving system.

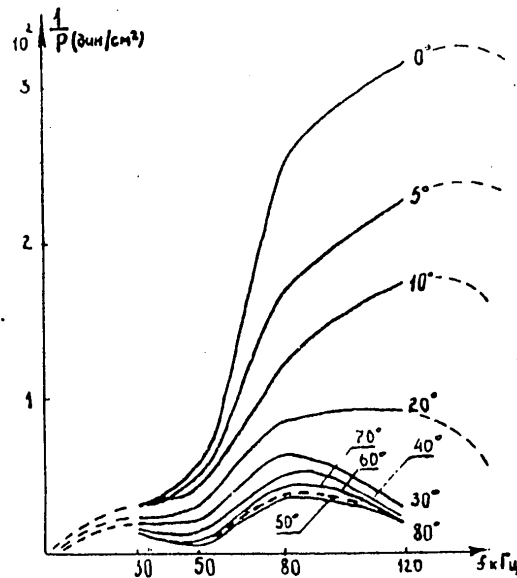


Figure 40. Transmission Characteristics of "Spatial-Frequency" Filters on the Horizontal Plane

Considering the fact that under real conditions the sound field is characterized by three-dimensional directivity, and not by cross-sections on the horizontal and vertical planes, it must be expected that when scanning it is possible to have a quite flexible "tuning" of the parameters of the spatial-frequency filters for a broad class of spectral characteristics. This in turn may be an efficient device in processing the acoustic information when classifying various underwater objects.

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The receiving system using optimum filtration is invariant to a change in amplitude, time lag and phase of the signal. It is insensitive to signals that have a different spectrum or those coming from different directions in relation to the source of the useful signal. It is possible that it is precisely in the optimum processing, carried out according to the principle of spatial-frequency filtration of the signals that the explanation is found for the high degree of resistance to interference and efficiency of the sonar system during detection and recognition. Obviously, at the present level of knowledge, with a relatively large amount of experimental data, the need has become urgent for an approach to studying the dolphin's locator as an integral system, functionally related in all its units. The attempt to reduce the data from our studies into a unified chain of elements of sonar leads to the conclusion that the dolphin's sonar system, inferior with respect to many characteristics of individual units of this system to technical analogs, as a unified whole is a highly specialized adaptive system, capable of solving problems that not a single technical device can approach.

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