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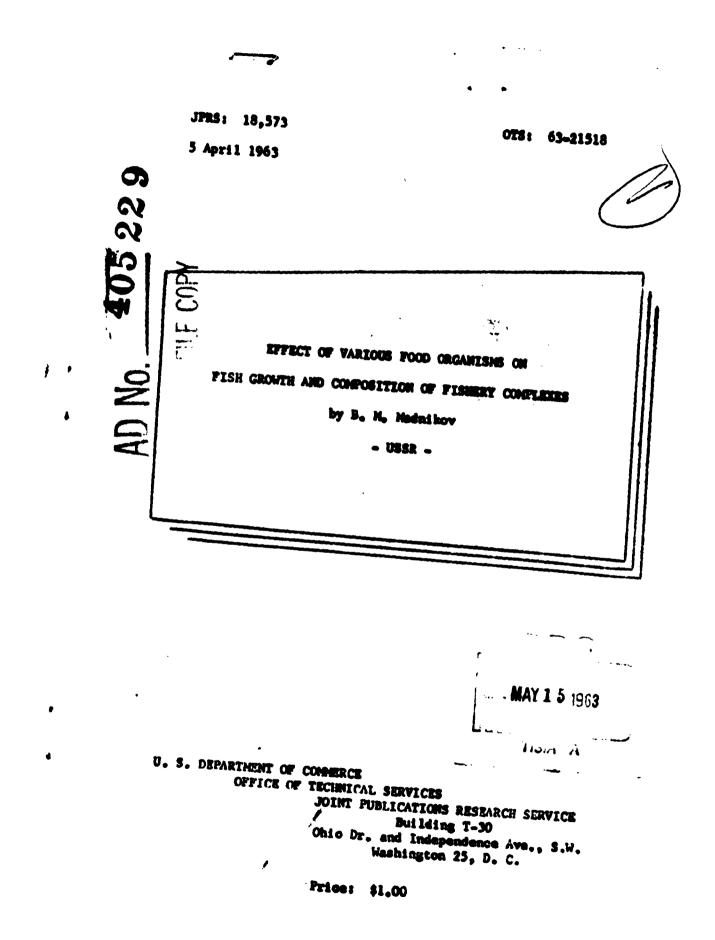
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FOREWORD

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EFFECT OF VARIOUS FOOD ORGANISHS ON FISH GROWTH AND COMPOSITION OF FISHERY COMPLEXES

[Following is a translation of an article entitled "Differences in Biological Cheracteristics of Food Organisms as a Factor Determining Fish Growth and the Composition of Fishery Complexes", by B. M. Mednikov" in the Russian-Language journal <u>Vopresy Inhticlesii</u> (Problems of Ichthyology), Mescow, Vol 2, No 2, 1962, pp 299-308.]

The question of factors which influence the rate of growth of fishes is still open to discussion. Numerous investigations carried out by various authors have been unable to clarify conclusively which factors should be considered as determining ones, viz., abiotic (temperature, salinity, etc.) or biotic ones (for example, quantity, caloricity and accessibility of food objects). Undoubtedly, such a complex phenomenon as growth of the organism depends on a number of factors and each of them, under definite con-

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ditions, may become a determining factor. The present work is devoted to the analysis of one of the factors determining the growth of pelagic fishes which, apparently, has not been given proper attention up to now.

For several reasons, it will be more convenient to begin from a concrete example. I.I.Nikolayev (1956), while studying the causes of slow growth, fattiness and repid sexual maturation of the Baltic "salaka" herring (Clupea harengus membras L.), arrived at the conclusion that this phenomenon cannot be explained by the lack of food, since the plankton of the Baltic Sea is sufficiently abundant. Factors causing a slow growth of salaka, according to I.I.Nikolayev, are low winter temperatures (below 2°) at which salaka does not feed. Winter intermissions in feeding bring about the fact that four-year old salaka hardly attains 16-17 om in length, while Norway herring of the same age reaches 29-30 cm.

The hypothesis of I.I.Nikolayev is undoubtedly well-grounded. Nevertheless, it does not explain a number of facts. In particular, in the Baltic Sea, apart from a small herring species, there is also found the so-called giant salaka (Riesenströmling) reaching 27-28 cm of length in its fifth year of life (Svetovidov, 1952). Another

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planktophage of the Baltic Sea, vis., Baltic spratt (Sprattus sprattus balticus Sohn.) reaches 12-13 om in length at three years of age (Svetovidov, 1952; Kasanova, 1960), while a related form - S. sprattus phalericus (Risso) living in the Black Sea hardly attains 7-9 om in length (Svetovidov, 1952; Aslanova, 1954). Why, then, does the thermal regime of the Baltic Sea not prevent the growth of the big race of Baltic salaka or spratt? We will add that the herring of the Penzhinskiy Bay of the Sea of Okhotsk, the thermal regime of which is incomparably severer, displays a considerably higher rate of growth, viz.:

Age	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+
Longth, mm : Salaka (Kopor- skaya Guba) Ponzhinskaya herring		143	157	171	179	184	-	-	-	-
(according to Svetovidov, 1952)	62	129	183	227	258	279	294	305	316	325

It is significant that in the second year of life salaka is bigger, but subsequently Penshinskaya herring outstrips it. These facts, as well as a number of similar facts

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cause us to assume that the principal factor determining in the rate of growth and maximal dimensions of pelagic fishes is the qualitative composition of their food, or more exactly the size and weight of objects serving as their nutrition.

At present, the majority of researchers (Greze, 1939, et al.) agree that plankton-eating fishes, with rare exceptions, are not passive filtrators, as assumed, for example, by Wunder (1932), but catch the food objects one by one. They differ from predatory fishes (Ivlev, 1955) only by size of the preferred objects of food. According to V.S.Ivlev, the measure of asymmetry[#] of the curve of the occurrence of hoterodimensional organisms in the ration of planktophages is positive, while in the case of predatory fishes it is negative. Consequently, the overwhelming majority of pelagic fishes must be considered as prehensors (Beklemishev, 1952) or hunters (Zernov, 1949). As we already noted, filtrators are rare. These are the silver carp (Lypophthelmichthys molitrix, Val) feeding on phytoplankton

The measure of asymmetry S is obtained from the formula $S = \frac{\sum_{n=1}^{3}}{n \sigma^{3}}$, where a designates deviations from the mean size of preys, σ is root-mean-square deviation, and n is the number of variants.

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(Borutskiy, 1950), the paddlefish (Polyodon spathula Wald.) (Kofoyd, according to Nikol'skiy, 1954), and the basking shark (Cetorhinus maximus Gunn.). The feeding of the latter species is similar to the feeding habits of baleen whales.

It is interesting to note that actively moving filtrators are encountered only among small animals (Rotatoria, Copepoda, Cladocera, Mysidacea, Appendicularia), as well as among the largest ones (whales); animals-filtrators which fill this dimensional break are sessile or little mobile. It is possible that straining of food is, from the energy viewpoint, convenient only for the largest and smallest . mobile animals. But at present we are interested in prehensors. The analysis of a number of works by V.S.Ivlev (1914). 1945, 1960 and others), in which the dependence of rations of fishes upon mean concentration of feeds, nonuniformity of their distribution and length of the "hunting path" is being discussed, prompts us to conclude that plankton-esting prehensors may feed on organisms having only definite dimensions; the upper limit of the size of prey is determined by the opening of the ostium and the lower one by the density of the straining net of gill rakers. At the same time, feeding with very small organisms even with the aid of retaining gill rakers is not advantageous for a planktophage since in the

case of corresponding dispersion of preys the energy out lay for their search is not compensated for by the energy contained in a ration. Hence, it follows that a pelagic fish may grow to a definite size only in the presence of corresponding feed organisms since feeding on other organisms is either physically impossible or is not advantageous in terms of energy. From this viewpoint, let us examine the nutrition of salaka and other pelagic fishes according to the usual dimensional groups of their feeding objects:

1) mesoplankton (Copepoda, Cladocera and others), dimensions of a few millimeters or less;

2) macroplankton (Euphausiidae, Hyperiidas, Mysidae), dimensions of the order of 1-3 cm;

3) micronekton (shrimp's, large Gammaridae, immature fish), dimensions over 3 cm.

According to G.V.Boldovskiy (1941), herring of

"The length of the "hunting path" (l) does not increase proportionally to the smallness of preys since it increases according to the formula $l = v(t_a + t_b)$, where v is the mean speed of fish during feeding; t_a is the time spent in hunting; t_b is time spent in prey swallowing (Ivlev, 1944). Naturally, t_b can never be equal to 0, or even approach it.

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the Berents Sea, fattening under conditions which we consider as optimal ones for the given species, feeds mainly on Euphausiidae (65% of alimentary bolus) and Calanus finmarchicus of IV-V stages (27.6%). Transferred into the Baltic Sea, the North Atlantic herring encounters different conditions since in this water body there are no Ruphausiidae and large Calanoida. The largest copepods of the Baltic Sea, viz., Limnocalanus grimaldii and Pseudocalanus elongatus, hardly reach 0.35 and 0.087 mg (Bodnek, 1953) and the other forms (Acartia, Centropages, Eurytemore. Bosmina) are still smaller. Before reaching 10-11 cm in length, the Baltic herring is compelled to feed on small crustaceans passing thereafter to nektobenthonic Mysidae replacing Euphasiidae (Sushkina, 1953) (Fig. 1). Finding oneself in such conditions, the herring may adapt itself to them in two ways: it may change into small, rapidly maturing salaka, since a further growth is not advantageous from the energy viewpoint, or, preserving a high rate of growth, it may become a predatory fish consuming micronekton. In fact, a giant salaks feeds on stickleback, immature salaka and spratt (Schneider, 1908; Svetovidov. 1952; Berg, 1948); there is no doubt about its predatory way of life.

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Fig. 1. Food composition and dimensions of Hurmansk herring (Clupes harengus harengus Linne) (a) and Baltic salaka (b) on the fourth year of life (according to Boldovskiy, 1941 and Sushkina, 1953). 1 - mesoplankton; 2 - macroplankton; 3 - micronekton. Dashed curve - absolute length of the fish.

It is possible that a similar way of adaptation to different feeding objects was responsible for differentiation of herrings inhabiting the White Sea into small and large races. All the diverse White Sea herrings (Tambovtsev, 1957) may be subdivided into small ones maturing in the 2nd-3rd year and large ones maturing in the 4th-5th year of life. A similar analogy between salaka and White Sea herring is also pointed out by N.A.Dmitriyev (1958).

The interdependence between the growth of pelagic

Fishes and composition of their food may be most clearly traced in the case of Caspian Clupeidae of Alosa and Clupeonella genus. Small Caspian mesoplankton (Eurytemora grimmi, Calanipeda aquaedulcis, Cercopagis, Evadne) is consumed by Clupeonella delicatula caspia Svet., reaching 60-90 mm in length (Barysheva, 1951). With increase of the dimensions of Caspian representatives of the Alosa genus, mesoplankters disappear from their diet, and then macroplankters (Mysidae). The largest Caspian herring - blackbaoked shad (Alosa Kessleri kessleri) - is a fish of prey which consumes mainly C. delicatula (Fig. 2).

All the abovesaid is not new. G.S.Karzinkin (1952) convincingly demonstrated that grown-up young pickerels can already feed on plankton. Cases are known (Tyurin, 1935) when perch living in lakes where no other fish are present subdivides into a small race feeding on plankton (usually males) and a large race (usually females) consuming small representatives of its own species. Already in the 10th stage of its development (45-60 mm of length), the sander becomes a fish of prey, although it can use shrimp and Mysidae if they are available in a water body (Konstantinov, 1955), and its growth is delayed if macronektonic organisms are unavailable, as pointed out by N.I.Syrovatskaya (1959).

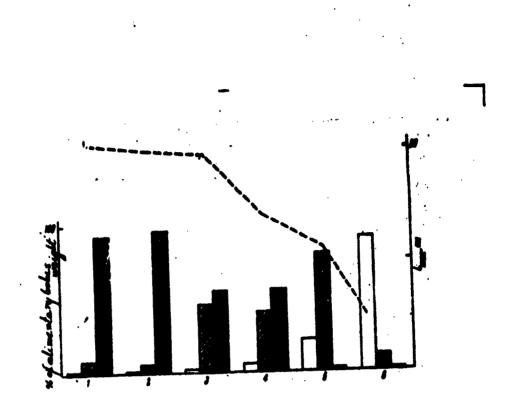


Fig. 2. Composition of food and maximal dimensions of Caspian pelagic fishes (according to Ostroumov, 1947; Svetovidov, 1952). 1 - Blackbacked shad; 2 - "Agrakhanka" herring (Alosa brashnikovi agrakhanika, Michailowsky); 3 -"Dolginka" herring (Alosa brashnikovi brashnikovi, Borodin); 4 - Big-eyed shad (Alosa saposhnikovi, Grimm); 5 - Caspian shad (Alosa caspia); 6 - Clupeonella delicatula caspia. Other designations are the same as in Fig. 1.

G.G.Vinberg (1956) calls this phenomenon the biological inequality of food value and suggests that "feeding on sooplankton, beginning from certain dimensions of fish, may be connected with a low rate of growth". The majority of researchers consider age variability of feeding as a function of growth: in fact, these phenomena are obviously interdependent.

Differences in the rate of growth of fish living under different conditions are satisfactorily explained by biologically different quality of feed organisms. Thus, for example, it becomes clear why lake forms of herrings having few vertebrae are smaller than oceanic ones; nineyear old Olyutorskaya herring reaches 40.7 cm of length, while herring of Nerpich'ye Lake attains 31.0 cm (Svetovidov, 1952). The same pattern is observed in landlocked and anadromous salmonidae consuming plankton. The sockeye (Oncorhynchus nerks) in the open sea reaches 56 cm in length, while the desh-water for in Kronotskoye Lake attains only 24.3 cm (Krokhin and Krogius, 1936).

The mass plankton organisms of continental water bodies are, as a rule, smaller than marine ones; this is especially true of the most important feed objects of fish, viz., copepods. Nost probably, it is exactly for this reason that plankton-eating fresh water-fish are much smaller than marine ones and, at the same time, they are characterized by a rapid maturation and short life cycle (Baltic lake smelt, bleak, cisco) or by a slow rate of growth (blue bream). The latter species living under very favorable feeding conditions of the Rybinsk water storage reservoir

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Freaches, at ten years of age, only 32 cm (Yurovitskiy, 1958). Exceptions from this rule are rare. Thus, for example, the Baikal omul (Coregonus automnalus migratorius Georgi) is considerably larger than other planktoneating coregonines. But, one must take into consideration that this species lives under fevorable conditions of Baikel Lake where the vegetative period is longer (Svetovidov, 1934), and where large pelagic crustaceans (Macrohectopus bramickii), or small ones (Epischura baicalensis) in large concentrations, develop. The data of Ya. 3. Potakuyev (1954) prove that the adult omul feeds on Epischura if the conisntration of this crustacean attains 30,000-35,000 per m²: if it decreases, the emul turns to a substitute food. At a population of Epischura below 10,000 per m³, the omul feeds on Amphipoda and immature Comephorus. Apparently, the outlay of energy in search of Epischura at this concentration is not compensated for by the energy of the ration even at the low temperature regime of Baikal Lake.

It is well known that warm-water (south-boreal and tropical) plankters, especially copepeds, are considerably smaller then cold water (lankters. A.K.Goynrikh (1961) points out that in tropical plankton Copepeda measuring 0.36-0.54 mm predominate, while dimensions of 0.54-0.91 mm are less often

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found: boreal Copepoda (Calanus finmarchious, C. cristatus, C. plumchrus) are 5 to 10 times larger. Hence, it follows that tropical and subtropical plankton-eaters should be considerably smaller than boreal ones. This is exactly what happens: according to T.S.Rass (1960), the main commercial species of plankton-eaters of north-boreal waters of the North Atlantic and North Pacific Oceans is the herring (maximal dimensions up to 50 cm); in the southboreal region such fishes predominate'as the sardine, spratt and anchovy, dimensions of which fluctuate from 15 to 25 cm. This phenomenon is expressed most sharply in tropical waters where, in addition to small plankton-eaters - Clupeidae, we have flying fish. Feeding on plankton is all the more disadvantageous for large tropical fish since the fat content in it sharply decreases (Bogorov, 1960), while on the contrary the outlay of energy for metabolism increases because of the high temperature of water despite the adaptive decrease of the intensity of metabolism (Vinberg, 1961).

This probably explains a decrease in the rate of growth of pelagic fishes living at the southern boundaries of their habitat. As an example may serve a decrease of the growth rate of the mackerel (Scomber scombrus L.) according to Aker (1961) and Lisaner (1937) in the latitudinal di-

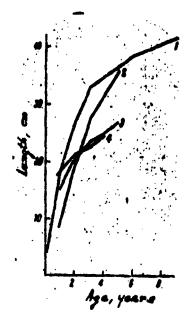


Fig. 3. Rate of growth of mackerel (according to Aker, 1961). 1 - North Sea; 2 - Brittany; 3 - Bosporus; 4 - Adriatic Sea

rection - from the North Atlantic Ocean to the Bosporus and Black Sea (Fig. 3). One may assume that the cause of the slow growth of the Black-Sea cold-loving forms (spratt, whiting) lies precisely in the food composition and not in the direct action of temperature fluctuations, as maintained by Yu.G.Aleyev (1956).

A direct consequence of the reduction in size of plankters and planktophages in warm waters is the increase in the population of fishes with mixed feeding and in that of medium-size fish of proy, feeding on small fish. We shall recall that in the Black See the saurel Trachurus trachurus is represented by a small plankton-feeding race, as well as by a large one of prey. A similar phenomenon was noted in respect to the Baltic herring.

All the abovesaid may be summed up as follows: with freshening and warming of the water reservoir, the planktonic organisms become smaller; as a result of this, the plankton-eating fishes also grow smaller. Naturally, the question arises of how to explain the reduction in size of plankters in warm and fresh waters. Of course, it is possible to assume that we are faced with the result of a direct effect of temperature (Bogorov and Preobrazhenskays, 1934). But another reason is also possible, vis., the growing smaller in low latitudes and fresh waters of representatives of the initial link of food chains phytoplankton. According to N.V.Morosova-Vodyanitskaya (1957), phytoplankton of the Black Sea may be divided into three dimensional groups:

1) cell dimensions over 50 μ - Diatomeae (Rhisosolenia, Coscinodiscus, Chaetocerus) and Peridineae (Geratium, Peridinium);

2) cell dimensions 20-50 μ - Diatomeae (Cyclotella) and Peridineae (Exuviaella cordata, Gonyaulax);

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3) cell dimensions less than 20 µ - Occeolithophoridae and smell Dinoflagellata.

In waters of seas with sharply expressed seasonal variations, there alternately predominate species of one or another group, but at higher latitudes the species of the first group, vis., large Distanese, prevail. The southboreal and especially freshened water reservoirs (Caspian Sea, etc.) are characterized by a predominance in phytoplankton of species of the 2nd group (Exuvisella cordata). Finally, in tropical latitudes, the main role is played by the smallest Coccolithophoridae, Flagellata and small Diatomeae (Riley, 1957; Hentschel, 1928). Thus, according to the data of Hasle (1959), at the experiment stations in the equatorial some there were encountered 42 species of Diatomeae, 53 of Dinoflagellata and 33 of Coccolithophoridae, whereupon the majority of Distances belonged to small species not exceeding 50 M. Exceptions (as the giant tropical Distomes Ethmodiscus rex) are comparatively rare.

"Their population may be small and sometimes it is smaller than that of Distomese (Hasle, 1960), but their yield is considerable because of rapid reproduction (NoroSova-Vodyanitskaya, 1957) Naturally, Calanoida of boreal waters are rough filtrators and prehensors (Beklemishev, 1954). Warm-water Calanoida, because of their inconsiderable dimensions and finer structure of filtrating apparatus, are capable of using smaller algae for food. A.K.Geynrikh (1958) points out that "in the tropical region, unlike in the moderate one, the plant-sating copepods are using, apart from Diatomsae, also Coccolithophoridae and Silicoflagellata to a considerable extent. At the same time, in contrast to the moderate latitudes, apart from comparatively large Diatomsae, also very small ones (less than 11μ in length) are being used."

The same author points out that in the nutrition of Calanoida 1 mm in length (predominating in the tropical plankton) there prevail Diatomeae smaller than 11 μ , i.e., belonging to the 3rd dimensional group. K.V.Beklemishev (1961) also arrives at the conclusion that "crustaceans of smaller dimensions do not consume or poorly consume large cells or cells grouped into colonies," while large Calanoida do not catch algae smaller than 10 μ .

In waters of Soviet south seas, where, depending on the season, various phytoplanktonic complexes are encountered, Calanoida capable of consuming algae of diffe-

Front sizes developed on a wide scale. Thus, the Black Seal Acartia clausi (Petipa, 1959) may consume Diatomese and Dinoflagellata measuring from 100 to 5μ . It is worth noting that Calanus helgolandicus - the largest copepod of the Black Sea - according to the same author (Petipa, 1960), consumes Noctiluca miliaris, which thus serve as an intermediate alimentary link between it and small algae.

The abovesaid compels us to assume that the cause of decrease in size of warm-water and fresh-water Galanoida is not a direct action of temperature but also of food composition. In connection with this, we shall note that fine filtrators, viz., Caladocera, are also characteristic of fresh waters. In the sea we observe a mass development of only such fresh-water species as Penilia evirostris which can filtrate particles not larger than 8 μ .

The question of the cause of the predominant development, in tropical and continental waters, of small but intensively reproducing autotrophic species still remains open. The temperature can hardly be the sole cause and, most probably, to explain this phenomenon it will be necessary to take into account also the seasonal fluctuations of illumination and biogenic elements.

The logical development of all quoted considera-

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tions is the following thesis: the length of alimentary chains of mass pelagic organisms increases from the poles to the equator. We will quote a few such examples. The most widely distributed planktophage of the Arotic basin is the polar cod (Klumov, 1937). According to the preliminary data of S.K.Klumov, it feeds on both phyto- and scoplankton; from the character of its diet, it should be considered as belonging to the second and third link of the alimentary chain. Almost all predatory fishes, pinnipeds and cetaceans (in particular, the white whale) of high latitudes of the Arctic feed on the polar cod. Therefore, the food chain beginning with primary producers, viz., phytoplanktonic algae, and ending with terminal links[#] (white whale), contains only 3-4 links:

phyto- and zooplankton - polar cod - white whale

The alimentary relations of the pelagic some of the boreal waters of the Atlantic and Pacific Oceans are mostly four-membered. The alimentary relationships of the herring feeding on planktonic crustaceans may serve as an "By terminal links of the food chain we understand animals eliminated from the water reservoir or entering the cycle of organic substance only in the process of posthumous destruction,

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example. The herring serves as food for sharks, dolphins and some striped whales. Naturally, this does not exclude the existence of shorter and longer chains.

In the tropical waters the alimentary chains are longest since zcoplankton serves here as food for small fish (sardines, anchovies) which are, in turn, consumed by large fish (tunas, predatory Glupeidae, golden mackerels) and squids. Fishes which, in low latitudes, reach the dimensions of the North Atlantic herring are no more planktophages but predatory fishes, i.e., they already belong not to the third but to the fourth link of the food chain. These organisms, in turn, serve as food for sharks and especially for large squids. In the tropics, there are no giant planktophages apart from rarely encountered whale shark Rhineodon. Baleen whales, wintering in warm waters, are not feeding here. The most widely distributed whale of the tropics, the sperm whale, feeds on the last links of the alimentary chains, viz:, giant squids and marks (Sleptsov, 1955).

In waters of high latitude of the Antarctic, we will find probably the shortest food chain leading from phytoplankton to giant planktophages. They are linked by the most common species of the Antarctic, the crustacean Euphausia superba. According to the data of Barkley (1940),

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This crustacean feeds almost exclusively on phytoplankton, while itself it constitutes the basic component of the diet of penguins, pinnipeds (orab-eating seal) and whales down to the largest of ever-existing animals, viz., the blue whale.

The theses developed in the present article are hypothetical to a great extent since they are not supported by appropriate calculations. This is caused by the deficiency of the present-day hydrobiological methodology which operates with the mean values of the population and biomass of alimentary objects. According to V.S.Ivlev (1955), the ration of the fish, r, may be expressed by the formula

 $-(kp + c\zeta)$ r = R·[1 - 10], where R is the maximally possible ration, p is density of prey population, k and c are proportionality coefficients, and ζ is the indicator of the aggregateness of prey distribution. In their works, the planktologists tacitly start from the condition that $\zeta = 0$, i.e., the feeding objects are distributed with absolute uniformity. But, this is far from being so. Practically, the larger the planktonic organism, the higher the indicator of its aggregateness; it is known that Euphausiidae, Mysidae and other macroplanktonic organisms

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Latay in flocks; & = 0 both for Copepode and Cladocers.

An approximate count (which is omitted) leads to a paradoxical conclusion; fresh-water plankton, under conditions of uniform distribution, cannot compensate for the outlay of energy for its conquest by fish of such size as the blue bream. Lake Chud whitefish or "ripus" (Coregonus albula ladogonsis). Hence, there is a clear necessity for determining the indicator of the aggregateness of alimentary objects of industrial fish. This value corresponds (Ivlev. 1955) to the mean-square deviation from the mean biomass, $\zeta = \sqrt{\sum a^2}$. On this basis, one may suggest the simplest method for determination of the aggregateness indicator: if, before, planktologists were content with taking one sample, now it is necessary to take several samples in one horizon and determine not only the mean biomass but also the deviations from it. The lack of time at experiment stations will probably not permit, in the majority of cases, the multifold increase of the number of samples and therefore it will be preferable to determine the indicator of aggregateness from the formula $\xi = \sqrt{\frac{\sum e^2}{\sum e^2}}$ (Urbakh, 1960). The minimal number of samples necessary for sufficient accurateness in determination of this value must be

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probably established empirically on the basis of suffi-

The second indispensable condition, as pointed out by V.S.Ivlev, is the correspondence of the volume of the sample to the area of a single feeding of the studied objects, and here we will have to establish this volume empirically. Naturally, a sharp increase of the number of samples to be processed will delay the processing of the material but this can also be avoided by applying repid methods of sample processing (Mednikov, 1961; Mednikov and Starobogatov, 1961).

In the present article, we deal with pelagic fishes but there is no doubt that biologically different qualities of food also exert an essential influence on the growth of benthophages. This is attested to, in particular, by the following fact. The roach, feeding on plankton and benthonic crustaceans, is characterized by slow growth as compared with roach of those water reservoirs where the basic component of its food are mollusks (Zheltenkova, 1949). In this case, the question is only complicated by other factors (presence of shelters and other forms of constitutional protectedness of prey); an analysis of these factors was given by E.V.Borutskiy (1960).

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The theses developed may be of practical significance in a number of cases. This is seen from the following example. As is known, in the Aral Sea there were practically no plankton-eating fish, and during the last decade the Baltic salaka was introduced into this water reservoir. The result of this measure was successful at first sight (Konovalov, Markova and Binting, 1958): salaka was transformed into a large, rapidly growing race of the type of "Riesenströmling." But all the authors who studied plankton on the Aral Sea noted its extreme quantitative and qualitative poorness. The data of N.K. Lukonina (1960) permit us to consider that the annual production of Aral plankton is tens of times less than the plankten production of the Sea of Azov - a water body of similar area, salinity and location. Hence, it is clear that planktophages in the Aral Sea are few , most probably because they cannot exist there. It is possible that salaka in the Aral Sea, besides amphipodans (Konovalov et al., 1958), consumes the young of other fishes. For this reason, the acclimatization of salaka (fish of low value but which can cause damage to valuable fish) in the Aral Soa was a thoughtless step, the success of which should be deplored more than would be its failure. Such

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Gases are not so rare. We shall recall, in particular, that northern whitefish transplanted into Lake Sevan likewise did not elect to feed on plankton but passed to feeding on amphipodans and became competitors of Sevan trout; accordingly, the rate of their growth increased.

All the abovesaid convinces us that the dimensions of fishes and their rate of growth, although are determined by alimentary relationships, cannot in all cases constitute a proof of the extent of the feeding base. In the same way, the biomass of the plankton, without considering the dimensions of plankters composing it and dispersion of their distribution, cannot characterize the conditions of feeding of planktophages. It seems to us that quantitative investigations in this direction would shed light on many unexplained features of the biology of fishes and other aquatic animals.

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