

## FISHERIES RESEARCH BOARD OF CANADA

Translation Series No. 1779

Seasonal dynamics of food competition  
of fish

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Original title: Sezonnaia dinamika pishchevoi konkurentsii  
ryb

From: Zoologicheskii Zhurnal (Zoological Journal), 25 (5) :  
441-449, 1946

Translated by the Translation Bureau (M.E.McL.)  
Foreign Languages Division  
Department of the Secretary of State of Canada

Fisheries Research Board of Canada  
Biological Station,  
St. Andrews, N. B.

1971

21 pages typescript

FRB 1779

DEPARTMENT OF THE SECRETARY OF STATE  
TRANSLATION BUREAU

SECRETARIAT D'ÉTAT  
BUREAU DES TRADUCTIONS

FOREIGN LANGUAGES  
DIVISION



DIVISION DES LANGUES  
ÉTRANGÈRES

TRANSLATED FROM - TRADUCTION DE  Russian	INTO - EN  English
--	--------------------------

AUTHOR - AUTEUR  
  
Shorygin A.A.

TITLE IN ENGLISH - TITRE ANGLAIS  
  
Seasonal Dynamics of Food Competition of Fish  
Title in foreign language (transliterate foreign characters)  
Sezonnaia dinamika pishchevoi konkurentsii ryb

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.  
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET. TRANSCRIRE EN CARACTÈRES PHONÉTIQUES.

Zoological Journal  
Zoologicheskii zhurnal

REFERENCE IN ENGLISH - RÉFÉRENCE EN ANGLAIS  
  
Zoological Journal

PUBLISHER - ÉDITEUR Hydrobiological Laboratory of the Institute of Marine Fisheries and Oceanography	DATE OF PUBLICATION DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL NUMÉROS DES PAGES DANS L'ORIGINAL  441 - 449
	YEAR ANNÉE	VOLUME	ISSUE NO. NUMÉRO	
PLACE OF PUBLICATION LIEU DE PUBLICATION  USSR	1946	25	5	NUMBER OF TYPED PAGES NOMBRE DE PAGES DACTYLOGRAPHIÉES  21

REQUESTING DEPARTMENT MINISTÈRE-CLIENT	Fisheries & Forestry	TRANSLATION BUREAU NO. NOTRE DOSSIER N°	0778
BRANCH OR DIVISION DIRECTION OU DIVISION	Fisheries Research Board	TRANSLATOR (INITIALS) TRADUCTEUR (INITIALES)	M.E.McL.
PERSON REQUESTING DEMANDÉ PAR	Dr. A.V. Tyler, Biological Station, St. Andrews, N.B.	DATE COMPLETED ACHEVÉ LE	MAY 13 1971
YOUR NUMBER VOTRE DOSSIER N°	769-18-14	UNEDITED DRAFT TRANSLATION Only for information TRADUCTION NON REVISÉE Information seulement	
DATE OF REQUEST DATE DE LA DEMANDE	21.1.71		

FLD 69A



FRB 1779

CLIENT'S NO. N° DU CLIENT	DEPARTMENT MINISTÈRE Fisheries & Forestry	DIVISION/BRANCH DIVISION/DIRECTION Biological Station	CITY VILLE St. Andrews, N.B.
BUREAU NO. N° DU BUREAU 0778	LANGUAGE LANGUE Russian	TRANSLATOR (INITIALS) TRADUCTEUR (INITIALES) MEMcL	DATE MAY 13 1971

## Zoological Journal

Vol. XXV

1946

No. 5

Seasonal Dynamics of Food Competition of Fish441.

A.A. Shorygin

UNEDITED DRAFT TRANSLATION

Only for information

TRADUCTION NON RÉVISÉE

Information seulement

VNIRO of Hydrobiology Laboratory

In two preceding papers [ 5, 6 ] a quantitative method of studying the food competition of fish was proposed by us. In the first one, devoted to study of the feeding and food relations of Caspian bullheads, a lack of data on the quantity of food used by the bullheads per unit of time forced us to compromise and only in the second paper were we able to describe our method in its pure form. Briefly it consists of the following. The strength of food competition between the species depends initially on two factors: firstly on the character of the food and secondly on the relation between the consumption of the food by both competitors and its availability. It is quite obvious that, all other conditions being equal, the food competition will be stronger, the greater the similarity in the diets of the competing species on one hand and the ratio between their use of the food for which they are competing and its availability on the other hand. It is evident that we must distinguish two characteristics of competition, namely: its volume and its intensity. By volume of competition we mean the ratio of that part of the food ration of the consumer-organisms for which they are competing to their total food ration. As for intensity, we mean by it the ratio between the consumption of the food for which the

the competitors are competing and its availability. As regards the resulting strength of competition, it must be in direct proportion to the volume as well as to the intensity of competition. It may therefore be expressed as the product of volume times intensity. To circumvent the difficulty arising from not knowing the rate of production of the food organisms, but only their biomass, a difficulty which prevents us from determining the intensity of competition over a protracted period, we proposed calculating the strength of food competition over a very short period, i.e. the momentary strength of food competition.

We expressed all this reasoning in two formulae:

$$E = e_1 + e_2 + e_3 + \dots + e_n,$$

when E is the total strength of food competition between two species, and  $e_1 - e_n$  the strength of food competition for separate species or groups of species of food organisms. These particular values can in turn be easily calculated according to formula

$$e = \frac{(a_1 + a_2) \times 100}{b}$$

when  $e$  is the strength of competition for separate species or a group of species of food organisms,  $a_1$  and  $a_2$  are respectively the daily consumption of these organisms by both competitors (calculated in terms of specific units of weight per bottom area of volume of water),  $b$  is the biomass of given food organisms in the same units  $d$  the degree of coincidence between the diets of the competitors with respect to the given food organisms (in percentages of this total food stock) and  $g$  the correction for the geographical location of the feeding areas of the competitors, (expressed in fractions of a unit). The first part of the formula  $\frac{a_1 + a_2}{b}$  gives us the intensity of competition; we deliberately multiply it by 100 in order to avoid large fractions. The second part of the formula -  $d \cdot g$  - gives the volume of competition.

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In order to simplify the calculations, it is more convenient to write the second formula as follows:

$$e = \left( \frac{100 a_1}{b} + \frac{100 a_2}{b} \right) \cdot d \cdot g$$

The strength of food competition calculated according to the given formulae is expressed in units which we named "konkalia". From the formulae it is not difficult to see that a strength of food competition, equalling on "konkalia" will occur whenever the competing species compete for one hundredth of their total food stock and when their daily consumption of this food also represents one hundredth of its supply.

By this method we were able to obtain a general picture of the food competition of eight commercial fishes of the northern Caspian Sea. The picture, however, was static and gave us no idea whatsoever of the dynamics of food relations. Yet, knowledge of at least the fundamental tendencies of these dynamics is no less important to us than knowledge of the static picture, since without it we cannot conceive those changes which are sure to come about in the food interrelations of fish, be it changes in the numbers of separate consumer-species or in the composition and size of their feeding areas.

Nevertheless, this side of food interrelations of fish, at least from a quantitative point of view, has not been studied at all to date. This was due to the lack of a quantitative method of study of the entire question of food competition as a whole. Apart from general observations and reasoning, nothing pertaining to the dynamics of food interrelations of fish has been published.

Zheltenkova was the first (3), while studying local and seasonal changes in the nutrition of Rutilus rutilus caspicus and Abramis brama and comparing the diets of both species, to turn her attention to a most interesting phenomenon. It turned out that in those regions and in those seasons during which one would, on the strength of the quantity of fish, size of the food supply and intensity of feeding, have assumed intensified competition between these two species, the similarity in the composition of their food was least. Wishing to verify this observation, Zheltenkova established the character of the food of Rut. rutilus caspicus and Abr. brama by the month (Table 1), something not done before. It turned out that the degree of resemblance between the diets of both species changes quite regularly, decreasing from spring to summer and increasing anew towards autumn. Hence, it turned

out to be least precisely in that period during which food consumption was greatest and during which the intensity of competition ought to be greatest. By means of figures Zheltenkova succeeded in establishing a very important law i.e. that the volume of competition is lowest when it is most intense. Hence one could assume the strength of competition to be more stable than its volume and intensity.

At present time we may add that growth in the intensity of food competition is accompanied not only greater divergence of the diets of the competing fish, but also by a divergence of the feeding areas. Indeed, in spring the feeding areas of Abr. brama and Rut. rutilus caspicus coincide much more closely than they do in the summer and autumn.

Nevertheless, what remains unknown is how the resulting strength of food competition changes in the end: does it remain unchanged because the divergence of the diets of the competitors and divergence of feeding areas compensates fully for the growth in the intensity of competition, or is this compensatory influence insufficient so that the strength of competition does grow with the increasing intensity, and if this is the case, then to what extent?

On the basis of our material, we have the opportunity to analyze this phenomenon more fully than did Zheltenkova and to answer the questions posed.

Thanks to the papers of Bokovaya [1, 2] and Krivobok [4] we have information on the seasonal changes of the daily rations of both Abr. brama and Rut. rutilus caspicus (Table 2). We can therefore go a lot farther in accuracy of calculation than we were able to when establishing the general picture of food competition.

Most difficult of all was determination of the quantity (by weight) of the competing species, especially since we had to establish these quantities on a monthly basis. On the advice of G.N. Monastyrski we accepted the following quantities of these species during the months which interested us (April - October) (Table 3).

In determining these figures the condition of the schools of both fish at the beginning and at the end of a given period, the

Table 1

Seasonal Changes in the Diets of *Abramis brama* and  
*Rutilus rutilus caspicus* in Percentages (Northern Caspian Sea, 1935)

	Rut. rut. caspius							Abr. brama						
	IV	V	VI	VII	VIII	IX	X	IV	V	VI	VII	VIII	IX	X
Cumacea . . .	0,05	1,6	0,6	0,7	1,0	6,8	3,5	1,5	52,0	70,0	21,4	44,3	18,6	24,6
Gammaridae . . .	6,0	1,2	0,4	0,7	0,4	5,9	3,3	0,5	0,4	0,4	1,7	3,8	1,18	1,2
Corophiidae . . .	12,1	3,0	0,5	3,8	10,2	0,6	0,9	74,0	23,3	12,2	18,0	26,4	25,4	21,0
Mysidae . . .	0,01	0,1	0,02	1,6	0,05	0,6	3,3	0	0,67	2,3	17,0	1,1	5,8	4,6
Ad. cna . . .	71,8	26,3	16,6	1,6	1,8	15,4	20,7	0	12,0	2,3	22,0	3,1	14,0	30,0
Didacn. . . .	0,01	16,2	6,0	6,4	0,5	2,6	0,9	0	0	0,1	0	0	0,03	0,15
Monod. cna . . .	0,3	7,4	23,0	21,1	50,6	19,4	19,0	0,7	0,4	0,4	0	0	9,6	1,2
Cardium . . .	0	0	0	0,3	0,02	4,2	4,2	0	0	0,1	0	0	0	0
Dreissena . . .	8,3	39,6	49,5	53,0	29,8	45,0	38,0	1,5	3,1	2,6	0,92	2,3	3,9	1,2
Mytilaster . . .	0	0	0,04	0	0	0	0	0	0	0	0	0	0	0
Gastropoda . . .	0	2,8	2,4	4,2	5,1	1,3	1,4	0,003	0,4	0,01	1,7	3,1	2,1	0,3
Vermes . . . .	0,43	0,87	0,01	0,1	0,06	0,4	1,4	2,1	4,6	7,3	3,7	8,6	7,9	13,2
Chironomidae . . .	1,0	0,3	0,03	0,24	0,005	0,8	1,5	0	3,1	1,9	13,5	2,3	12,4	2,4
Pisces . . . .	0,03	0,05	0,9	0,34	0,4	0,2	1,9	1,5	0	0	0,37	0	0,07	0,15

periods and the intensity of their migrations from sea river for spawning, as well as the change in the intensity of fishing during different months were taken into account. Regardless of all this, these figures are merely approximate; their fluctuations, however, are so insignificant that they cannot noticeably distort the final result, even if some errors had been permitted to occur in determining these fluctuations which are the substance of this discussion.

Table 2

Seasonal Changes in the Feeding Intensity of Rutilus rutilus caspicus and Abramis brama (daily consumption of food in percentages of weight of the fish)

Species of Fish	Months						
	IV	V	VI	VII	VIII	IX	X
Rut. rut. caspius . . .	3,5	3	4	4,5	5	4,5	4
Abr. brama . . . . .	2,5	1,5	2	2,5	3	2,7	2,5

Table 3

Quantity of Abramis brama and Rutilus rutilus caspicus in the Northern Caspian Sea in 1935 on a Monthly Basis (g/m<sup>3</sup>)

Species of Fish	Months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Rut. rut. caspius . . .	1,0	1,0	1,0	7,1	10,6	17,3	14,9	13,6	6,8	5,9	1,0	1,0
Abr. brama . . . . .				1,5	2,0	6,2	7,4	5,6	4,0	3,0		

As concerns data on the quantity of food animals, we only had average figures for each of the three seasons included in the study. We established their quantities per month by way of geometrical interpolation of seasonal data. We did the same with the data on the divergence of the feeding areas of both competitors.

Subsequent calculations were done the same way as when establishing the statics of food competition.

The determination of the volume of competition once again presented no difficulties. As before we did not take into account the content of soil in the digestive tract. Besides that we had to discard Cardylophora caspia and fish, since we did not have any reliable data on the hydroid biomass and we did not know which particular fishes were being discussed in a given case. As a result of this our figures differ somewhat from those of Zheltenkova. In establishing the general picture of the competition of fish, we already knew that the quantity of Mysidae was underestimated in bottom grab samples and we had to introduce a supplementary correction for this underestimate. In the given case we made this correction at the very beginning. At the end of the calculations a correction for the relative locations of the feeding areas was finally introduced. Data thus obtained is shown in Table 4 and in Fig. 1.

In order to be able to compare not only the course of the changes, but also the intensity of the fluctuations of individual elements, all curves in Fig. 1 are given on the same scale - in percentages of the average for each of them. We see that the picture, as expected, turns out to be not nearly as simple as we had outlined at the beginning. In order to understand the biological significance of the results obtained, we shall have to analyze them in detail. From April on to May the intensity of competition between Abramis brama and Rutilus rutilus caspicus decreased, but similarity in the diets increased. This occurred because in April Rut. rutilus caspicus consumed more Corophiidae (one of the basic food objects of Abr. brama) than in all other months which, as shown by Zheltenkova, is connected with the maturing process of sex cells products in the greater

Table 4

Seasonal Changes of Food Competition between *Abramis brama* and *Rutilus rutilus caspicus* (Northern Caspian Sea, 1935)

	Months						
	IV	V	VI	VII	VIII	IX	X
Volume of competition (in percentages)	14,9	22,1	7,0	11,7	18,9	38,3	35,5
Intensity of competition Correction for the loca- tion of feeding areas	2,9	1,9	7,4	16,9	24,0	8,6	4,2
strength of competition (in "konkalias")	1	1	0,9	0,50	0,34	0,3	0,3
	43	42	47	99	154	99	45

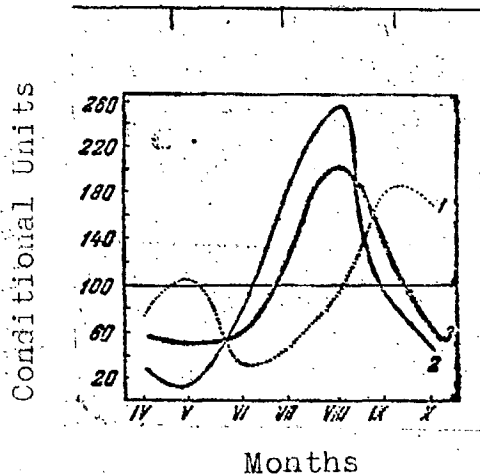


Fig. 1. Seasonal Dynamics of Food Competition between Abr. brama and Rut. rutilus caspicus

- 1 - volume of competition;
- 2 - intensity of competition;
- 3 - strength of competition.

part of the school. It was precisely these organisms which were the principal cause for the development in April of keener food competition between Abr. brama and Rut. rutilus caspicus. But in May the Rut. rutilus caspicus largely abandoned consumption of Corophiidae, the proportion of which in its diet dropped fourfold as compared to

April (from 12.1% to 3%). As a result the intensity of competition in May fell approximately by one and a half times and in return the similarity in the diets of the two species increased proportionately. This rapprochement occurred basically because of increased consumption of Adacna by Abr. brama, the competition for which however was considerably less keen than it was for Corophiidae. As a result of all this and in spite of the accelerated rate of feeding, the resulting strength of food competition between the Abr. brama and Rut. rutilus caspicus remained unchanged from April on to May (43 and 42 "konkalias"). In June the intensity of nutrition increases sharply (at that time the daily ration of Rut. rutilus caspicus increased from 7.1 to 17.3 and that of Abr. brama from 1.5 to 6.2, in percentages of the weight of the fish), and consequently the consumption of food as well, which led to a rapid increase in the intensity of competition. In accordance with this the similarity in the diets of both species too began to decrease almost as fast. As a result in June too the strength of competition remained almost at the same level as it had been during the two preceding months, increasing only very weakly (from 42 to 47 "konkalias"). Up until now the process has gone exactly as was conjectured by Zheltenkova. On the basis of our not very accurate calculations, one could hardly have expected a more complete quantitative confirmation of her ideas.

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As of July, however, the course of the process changes drastically. From June to August the intensity of competition continues to grow rapidly. This is explained by the continued growth of the intensity of nutrition of the Abr. brama during July (the biggest daily rations of Rut. rutilus caspicus were observed in June, those of Abr. brama in July) and thus, mainly by the rapid drop in the quantity of most food organisms, especially of those preferred by the fish.

Thus the increase in the intensity of food competition is understandable. But the volume of competition, i.e. the similarity in the diets of Abr. brama and Rut. rutilus caspicus not only does not decrease accordingly, as would have been expected, but on the contrary it too begins to grow, although not as fast as the intensity. As a result the strength of food competition between Abr. brama and Rut.

rutilus caspicus which, as we saw, had remained at roughly the same level until now, begins to augment quickly as well and by August reaches its maximum. Even the incipient divergence in the feeding grounds of the two species is unable to halt this growth, it merely retards it.

The change in the course of the process during this period of intensive nutrition is explained as follows. Rut. rutilus caspicus and Abr. brama compete not only with each other. They compete with other species as well and although Abr. brama appears to be the chief competitor of Rut. rutilus caspicus, it has a still stronger competitor itself, namely Gobius fluviatilis pallasii [7]. Besides, it is summer that food competition between Abr. brama, Rut. rutilus caspicus, sturgeons and even the pike perch (Lucioperca) ought to grow to a considerable degree as well. Indeed, analysis of seasonal changes in the diets of fish showed that in the summer Acipenser stellatus, as well as well as Acipenser and Lucioperca, switches largely to a diet of crustaceans. Acipenser in particular switches at this time to a considerable degree to a diet of Corophiidae which in this period makes up over one third (37%) of all its food. At that same time this group, as we already saw (Table 1), represents one of the two basic food groups of Abr. brama.

Under the pressure of growing competition for crustaceans with G. fl. pallasii and sturgeons, Abr. brama begins to switch to a diet of mollusks, mainly those which are also best liked by Rut. rutilus caspicus, namely Adacna. Indeed, if in the first two months (April - May), during which as a result of low intensity of nutrition and large dimensions of the feeding area, the food competition stood at a low level, the mollusks comprised no more than 15% (8% on the average) and Adacna no more than 12% (6% on the average) of its food, then during the following three months, corresponding to the period of heightened competition, the proportion of mollusks rose to 25% (11% on the average) and Adacna to 22% (8% on the average), i.e. was one and a half times higher than for the first period. Besides, during June - August there also was a sharp rise in the strength of competition because of crustaceans, especially because of Cumacea. This may be explained by Cumacea being

of great importance in the nutrition of Abr. brama (up to 70%) during that particular month, as well as by a decrease in their quantity in the benthos as a result of their being eaten up by fish, by those same bullheads in particular. Added to this in August was another very high level of competition for Corophiidae which in that month constituted quite a considerable part of the food of Abr. brama (26.4%), as well as Rut. rutilus caspicus (10.2%).

As a result of this the similarity in the diets of Abr. brama and Rut. rutilus caspicus began to increase in spite of the continued growth of the intensity of their competition with each other. The similarity, and consequently also the volume, increased meanwhile, though to a lesser degree than could have been expected, considering the changes in the diet of Abr. brama which were taking place. The point is that under pressure of growing competition from Abr. brama for Adacna, the diet of Rut. rutilus caspicus changed as well; Rut. rutilus caspicus began to desist from feeding on Adacna and increased its consumption of such mollusks as were consumed by Abr. brama, i.e. Monodacna and Dreissena, only to an inconsiderable degree.

In the period of heightened competition, Abr. brama, and under its pressure Rut. rutilus caspicus also was forced in this manner to switch to a greater degree than before to a replacement diet. However, the indicated changes in the feeding habits of Rut. rutilus caspicus could not fully compensate for the corresponding changes in those of Abr. brama, and from June to August the similarity in the character of their diets increased, in spite of the fact that the intensity of competition continued to grow at the same time. As a result, the strength, of competition between Abr. brama and Rut. rutilus caspicus increased as well and in August, as already mentioned, reached its maximum. As of that moment the situation changes once more. At the end of the period of nutrition a rapid drop in the intensity of nutrition and the resulting incipient restoration of food stocks reserves lead to a very fast drop in the intensity of food competition between Abr. brama and Rut. rutilus caspicus. The volume of competition, however, i.e. the similarity in diet continues to increase rapidly,

but this time basically on account of changes in the diet of Rut. rutilus caspicus which increases its consumption of Cumacea and Gammaridae. As a result of this, as well as the fact that Abr. brama still continues to feed extensively on mollusks, the strength of competition between the two species in September, in spite of a considerable drop, remains at a fairly high level. In this period of diminished strength of competition, the dynamics of its intensity and volume thus again are in inverse proportion. In September, at last, the continuing rapid drop in the intensity of nutrition leads to a further lowering of the intensity of competition and a diminishment of its strength, which returns to the level it was at when the feeding season began. The very weak drop in the volume of competition between Abr. brama and Rut. rutilus caspicus which occurred during that time is attributed to the decreasing similarity in their diets as regards mollusks (from 28% to 23%), just as the similarity with respect to crustaceans even increased somewhat (from 8.2% to 8.9%). Hence, it also is in complete agreement with the general course of the process.

The general picture of the dynamics of reciprocal food relations of Rut. rutilus caspicus and Abr. brama thus turned out to be fairly harmonious, biologically easy to explain and plausible. By taking into account the generally low accuracy of our calculations, we must admit that the results obtained surpassed our boldest expectations. In particular, not only did they permit us to confirm the correctness of the suppositions made about the reciprocal influences between various elements of food competition, they also allowed us to project those conditions under which this reciprocal influence becomes distorted, as well as the actual degree of such distortion.

At present the dynamics of reciprocal food relations between two fishes in their pure form, i.e. without the disturbing influence of other competitors, appear to be as depicted in the following sketch (Fig. 2).

Whether as a result of an increase in the intensity of nutrition or a decrease in the dimensions of feeding areas, or finally, as a result of the increased numbers of the competitors themselves, as

the intensity of the food consumption and along with it the intensity of the competition begin to increase, the similarity in the feeding habits of the competitors (the volume of competition) begins to diminish. The fish switch, as far as possible, to a diet of various organisms. From the beginning (apparently during the changeover from their favourite food to a substitute this divergence of the diets occurs with approximately the same intensity as does the

growth of competitive intensity, and as a result of this the strength of competition remains approximately at the same level, and even should it increase, it is only very insignificantly. As the intensity of competition increases further, the divergence of the diets of the competitors continues, albeit more slowly. It is apparent that this coincides with the changeover of the biologically less active competitor to emergency diet. But in this same period begins the intensive divergence of the feeding areas by both species (apparently, where this is possible). As a result of all this the strength of competition begins to increase already more strongly than it did in the preceding period, however the pace of this increase is not yet very great, since the divergence of the diets, which is amplified by the divergence of the feeding areas, still continues to exert its influence.

However, in the event of further growth of competition, even after the changeover to an emergency diet, the divergence of the diets of the competitors slows down even more, and the divergence of the feeding areas which by this time is already close to its possible limit, also slows down. As a result the strength of competition begins to

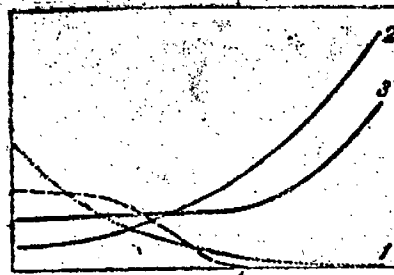


Fig. 2. Diagram of the Dynamics of Food Competition between two fishes.

- 1 - volume of competition;
- 2 - intensity of competition;
- 3 - strength of competition;
- 4 - degree of coincidence of the areas used for nutrition.

grow quickly, lagging only very slightly behind the growth of the intensity of competition. In the end, there may come the critical moment when, as a result of the continuing growth in the intensity of competition, the similarity in the diets of both competitors disappears altogether. Each of them will switch to a diet of completely different organisms. The volume of competition has become zero. The product of intensity times volume, i.e. the strength of competition, also came down to zero. The same may occur in the event of complete divergence of the feeding areas. However, it does not follow from this that competition between the two species has ceased. From being visible it has merely become invisible. From being kinetic, to use an analogy, it has become potential.

In the event of a lowering of the intensity of competition the entire process will of course proceed in reverse order. It is quite obvious that everything we have said is only a most general scheme. It is further quite obvious that, depending on the biological plasticity and the biological activity of the competitors, the ratio of their numbers, the size and composition of their food resources and finally, depending, also on other conditions and on the character of the body of water itself, individual aspects of the process will vary. Thus it is quite possible that in large bodies of water the divergence of feeding areas will be of predominant significance in equalizing the strength of competition, and that in small, densely populated bodies of water the influence of that divergence will be minimal. However, the general direction of the process, according to our conviction, will remain the same everywhere on the indispensable condition of course that the pair of species taken by us will not have any other strong competitors. The fewer of these competitors there will be, the less will be their influence, and the closer to the charted scheme will run the course of the entire process. If other strong competitors are present, though, the entire course of the process may change in essence; it may for instance turn out that the intensity and volume of the competition will begin to change parallelly. We became convinced of such possibility from the example of seasonal changes in the reciprocal food relations of Abr. brama and Rut. rutilus caspicus in the northern part of the

## Caspian Sea.

Nothing we have said here is new in essence having been long known to fish culturists. Known in particular are instances where, for example, Abr. brama, under the influence of competition from Ascerina cernua, changed over to a typical diet of planctonic crustaceans and where, as a result of this, competition between them completely or almost completely changed over to its potential form. But in spite of all the shortcomings in the material at our disposal, we managed nevertheless to give the entire phenomenon of food competition and its dynamics some kind of a quantitative appraisal, albeit a purely conditional one.

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