

Chapter II

THE STRUGGLE FOR EXISTENCE IN NATURAL CONDITIONS

(1) Before beginning any experimental investigation of the elementary processes of the struggle for existence we must examine what is the state of our knowledge of the phenomena of competition in nature. The regularities which it has been possible to ascertain there, and the ideas which have been expressed in their discussion, will help us to formulate correctly certain fundamental requirements for further experimental work.

In thorough field observations the fact which strikes the investigator most of all is the extreme complexity of the communities of organisms, and at the same time their possession of a definite structure. On the one hand they undergo changes under the influence of external environment, and on the other the slightest changes of some components produce an alteration of others and lead to a whole chain of consequences. It is difficult here to arrive at a sufficiently clear understanding of the processes of the struggle for existence. Elton writes for instance: "We do not get any clear conception of the exact way in which one species replaces another. Does it drive the other one out by competition? and if so, what precisely do we mean by competition? Or do changing conditions destroy or drive out the first arrival, making thereby an empty niche for another animal which quietly replaces it without ever becoming 'red in tooth and claw' at all? Succession brings the ecologist face to face with the whole problem of competition among animals, a problem which does not puzzle most people because they seldom if ever think out its implications at all carefully. At the present time it is well known that the American grey squirrel is replacing the native red squirrel in various parts of England, but it is entirely unknown why this is occurring, and no good explanation seems to exist. In ecological succession among animals there are thousands of similar cases cropping up, practically all of which are as little accounted for as that of the squirrels" ('27, p. 27-28). All this suggests that an analysis must be made of comparatively simple desert or Arctic communities where the number of components is small. Such a tendency to examine certain *elementary phenomena* is clearly seen in the following words of a Russian zoologist, N. Severtzov, written as far back as 1855: "It seems to me that the study of animal groupings in small areas, the study of these *elementary faunas* is the firmest point of support for drawing conclusions about the general laws regulating the distribution of animals on the globe."

However, besides this first possibility of studying competition phenomena among a small number of components, an active

intervention into natural conditions by means of biotic experiments may also be very important. Among such experiments the most frequent ones consist in the transportation of animals into countries new to them, which commonly leads to a great number of highly interesting processes of the struggle for existence (Thomson, '22). The second type of biotic experiments is an "exclusion" of the animal from a certain community. Further on we give some examples of the struggle for existence observed by such methods, but so far none of them have been sufficiently studied.

TABLE I
Number of fir trunks on a unit of surface under different conditions
From Sukatshev ('28)

Type of life conditions	20 years age		60 years age	
	Predominant trunks	Oppressed trunks	Predominant trunks	Oppressed trunks
I	5600	-	1300	640
II	5850	-	1600	680
III	6620	-	1950	650
IV	7480	-	2280	720
V	8400	-	2780	760

(2) It fell to the lot of botanists to have to deal with the simplest conditions of competition, and they arrived at a very instructive conception of the *intensity of the struggle for existence*. Foresters were the first to be confronted with the question of competition when they began to estimate the diminution in the number of tree trunks accompanying forest growth in different conditions of environment. They characterize the struggle for existence by the percentage decrease in the number of individuals on a unit of surface in a certain unit of time. At first sight one might think that the better the conditions of existence the less active is the struggle for life, and the greater the number of trunks that can survive with age on a unit of surface. Let us, however, look at the data of the foresters. For an example we will give in Table I the number of the fir trunks in the government of Leningrad (Northern Russia) corresponding to five different types of life conditions (Type I represents the best soil and ground conditions; V, the worst ones).

These data show, contrary to our expectations, that the better are the soil and ground conditions, the more active is the struggle for life, or in other words the smaller the number of trunks remaining on a unit of surface and, consequently, the greater the percentage of those which perish. If we think out this phenomenon, it becomes quite understandable: the more favorable the environment is for the plants' existence, the more luxuriant will be the development of each plant, the sooner will the tops of the trees begin to close above, and the earlier the oppressed individuals become isolated. Also, in better conditions of existence, every individual in the adult state will be more developed and occupy a greater space, but the individuals will be fewer in number. Investigations show that this is a general rule for all the forest species (Sukatshev, '28, p. 12). Similar data were obtained by Sukatshev ('28) in experiments with the chamomile, *Matricaria inodora*, on fertilized and non-fertilized soil. In counting up the individuals remaining at the end of summer (August 17), the following decrease of the original number of individuals was ascertained (see Table II and Fig. 1).

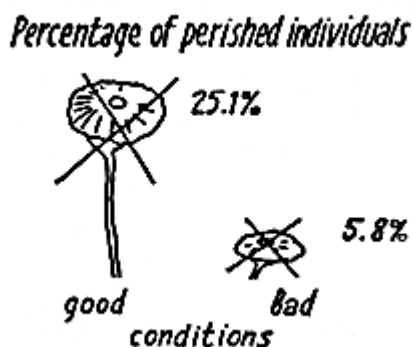


Fig. 1 Intensity of the struggle for existence in the chamomile *Matricaria inodora* on fertilized and non-fertilized soil (dense culture).

TABLE II

Decrease of the number of individuals in the chamomile (*Matricaria inodora*) expressed in percentage of the initial number
From Sukatshev ('28)

	PERCENTAGE
Dense culture (3 x 3 cm):	
Non-fertilized soil	5.8

Fertilized soil	25.1
Culture of middle density (10 x 10 cm):	
Non-fertilized soil.....	0.0
Fertilized soil.....	3.1

Here likewise in better conditions of existence competition proceeds with greater intensity, and the per cent of individuals which perish is greater.

The results obtained by botanists are certainly characteristic for the ontogenetic development of plants but at the same time they give us an approach to the quantitative appreciation of the intensity of the struggle for existence, the whole significance of which was already clearly understood by Darwin. In the next chapter we shall consider the struggle for life in animals, and there, using entirely different methods, we shall endeavor to formulate quantitatively the intensity of this struggle.

(3) In field observations the question often arises as to the struggle for existence in mixed populations, about which Darwin wrote: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera." Lately, botanists have tried to approach this problem experimentally. It became evident that, actually, in a number of cases competition is keenest when the individuals are most similar. The more unlike plants are, the greater difference in their needs, and hence some adjust themselves to the reactions of others with little or no disadvantage. This similarity must rest upon vegetation or habitat form, and not merely upon systematic position (Clements, '29). Researches on competition in mixed populations consisting of different kinds of cultivated plants were undertaken by many investigators (e.g., Montgomery, '12). Particularly interesting data concerning wild-growing plants have been recently published by Sukatshev ('27) in his "Experimental studies on the struggle for existence between biotypes of the same species." First of all he studied the competition between local biotypes of the plant, *Taraxacum officinale* Web., from the environs of Leningrad. These biotypes were cultivated in similar conditions with a fixed distance between the individuals, and the experiments led Sukatshev to the following conclusions: (a) One must rigorously distinguish the conditions of the struggle for existence in a pure population, formed by a single biotype,

and in a mixed population, consisting of various biotypes. (b) It is to be noted that a biotype which shows itself to be the most resistant in an *intra*biotic struggle for existence, may turn out to be the weakest one in an *inter*biotic struggle between different biotypes of the same species. (c) The increase in mutual influence of plants upon each other with an increase in density of the plant cultures, may completely reverse the relative stability of separate biotypes in the process of the struggle for existence. The biotypes yielding the greatest percentage of survivors under a small density of cultivation may occupy the last place in this respect in conditions of a dense culture. This can be illustrated by Table III.

TABLE III
Percentage of eliminated individuals in three biotypes, A, B and C of *Taraxacum officinale*
From Sukatshev ('27)

	RACE	SPARCE CULTURES	DENSE CULTURES
Pure cultures.....	A	22.9	73.2
	B	31.1	51.1
	C	10.3	75.9
Mixed cultures.....	A	16.5	77.4
	B	22.1	80.4
	C	5.5	42.0

If we arrange the biotypes mentioned in Table III according to decreasing stability, we shall find that in the conditions of a *not dense, pure culture*: $C > A > B$, i.e., the biotype C gives the smallest percentage of non-survivals and is the *most resistant*, whilst the biotype B is the weakest of all. In *dense pure cultures* the relations are entirely different: $B > A > C$, i.e., the biotype B is the most stable one. Lastly, for *dense, but mixed cultures*, we have: $C > A > B$. Almost similar data have been obtained by Montgomery ('12) in studying the competition between two races of wheat.

In another series of experiments Sukatshev ('27) studied the struggle

for existence between biotypes of various geographical origin (from various parts of U. S. S. R.), and inferred the following: (a) Judging by the percentage of non-survivals, one can say that in pure, as well as in mixed not-dense cultures, the dying-off is chiefly due to the influence of physico-geographical factors. Therefore, the biotypes originating from geographical regions strongly differing from a given region in their climate, turn out to be less resistant as compared with the local biotypes. But these relations can change under the influence of aggregation. (b) In dense mixed cultures, if we are to judge by the percentage of perished individuals, it is not the local biotypes that appear the most resistant in the struggle for existence, but those introduced from other regions. (c) The struggle for existence in mixed cultures of various biotypes is not so keen as that in pure cultures of separate biotypes with the same density.

The analysis of the struggle for existence in mixed populations of plants is now only at its very beginning. The exact data are few in number, but there exist numerous observations on the stratified distribution of plants (see Alechin, '26), considering these strata as a result of complex processes of competition and adaptation of the plants to one another in mixed cultures.

(4) Plants are also very favorable for the study of the influence of environment upon the struggle for existence in mixed populations. DeCandolle was already interested in this question in 1820, but as regards exact experimental researches very little has been done until quite recently when the works of Tansley ('17) and others appeared. These investigations show that in pure cultures two species can grow for a certain time on various soils, but each of the species has an advantage over the others in particular soil conditions. Therefore in mixed population in some soils the first species displaces the second, but in others the second species displaces the first.¹The actual relations existing here are, however, somewhat complicated (see Braun-Blanquet, '28).

¹Among animals such observations have been recently made by Timofeeff-Ressovsky ('33), who studied the competition between the larvae of *Drosophila melanogaster* and *Drosophila funebris* under different temperatures. We can mention also certain interesting data of Beauchamp and Ulyott ('32): "When *Planaria montenegrina* and *Pl. gonocephala* occur in competition with each other, temperature is the factor which governs the relative success and efficiency of the two species. *Pl. montenegrina* is the more successful at temperatures below 13-14°C. Above these temperatures *Pl. gonocephala* is the more efficient form."

The problem of the influence of environment on competition presents considerable interest, but as yet what we know is very meager. In the majority of cases it is observations of a qualitative character, of which we can give an example here: "The root-systems of the vegetation in the steppes of Southern Russia form, according to Patchosky, three

strata. The uppermost one consists of short roots belonging to annual plants which vegetate for a short time. The second, deeper-lying stratum belongs to the essential plants of the steppe vegetable covering, the Gramineae. The third, deepest stratum consists of the vertical stem-like roots of perennial dicotyledons (among them the steppe *Euphorbia*). Usually, the second gramineous stratum dominates. When, however, an immoderate pasturing takes place in a given locality, the gramineous covering begins to suffer and does not produce a vigorous root-system. Atmospheric precipitation can now penetrate to those soil horizons where roots of the dicotyledons are situated, and the latter begin to dominate. As a result appears an unbroken vegetable covering consisting of *Euphorbia*. Analogous results take place in case of increase in yearly atmospheric precipitation. In this case, although the water is energetically absorbed by the second gramineous root stratum, the rainfall is so considerable that a great part of the water penetrates deeper, contributing to the development of dicotyledonous plants. The large dicotyledons act depressingly upon the Gramineae, and they change places in respect to their domination" (Alechin, '26).

(5) The part which the quantitative relations between species at the beginning of their struggle play in the outcome of competition presents an interesting problem. Botanists do not possess exact quantitative data bearing on this question, and one meets only with considerations of the following kind: When new soils are colonized, if the species concerned do not sharply differ in their capacity for spreading, it mostly depends on chance which species colonizes the given area first. But this chance determines the further colonizing of the given locality. Even when the species that has first established itself is somewhat weaker than another species in the same habitat, it can for a comparatively long time resist its stronger competitor simply because it was the first to occupy this place. Only in case of a considerable weakness of the first comer will its domination be merely a temporary one, and the effect of the first accidental appearance will be rapidly eliminated (E. Warming ('95), Du-Rietz ('30)).

(6) Let us recapitulate briefly our discussion up to this point. Botanists have endeavored to investigate the struggle for existence by experimentation and under simplified conditions, but they are only beginning to analyze these phenomena. Their experiments are commonly limited to the process of ontogenetic development, and in only a few cases, chiefly concerned with competition in cereals, has displacement of some forms by others been traced through a series of generations (Montgomery ('12) and others). As concerns animals we have simply no exact data, and can only mention a few general principles which have been developed by zoologists in connection with the phenomena of competition.

One of these ideas is that of the "niche" (see Elton, '27, p. 63). A niche indicates what place the given species occupies in a community, i.e., what are its habits, food and mode of life. It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor. Curious examples of the existence of different niches in nearly related species have recently been obtained by A. N. Formosov ('34). He investigated the ecology of nearly related species of terns, living together in a definite region, and it appeared that their interests do not clash at all, as each species hunts in perfectly determined conditions differing from those of another. This once more confirms the thought mentioned earlier, that the intensity of competition is determined not by the systematic likeness, but by the similarity of the demands of the competitors upon the environment. Further on we shall endeavor to express all these relations in a quantitative form.

(7) The above mentioned observations of A. N. Formosov on different niches in nearly related species of terns can be given here with more detail, as the author has kindly put at our disposal the following materials from his unpublished manuscript: According to the observations in 1923, the island Jorilgatch (Black Sea) is inhabited by a nesting colony of terns, consisting of many hundreds of individuals. The nests of the terns are situated close to one another, and the colony presents a whole system. The entire mass of individuals in the colony belongs to four species (sandwich-tern, *Sterna cantiaca*; common-tern *S. faviatilis*; blackbeak-tern, *S. anglica*; and little-tern, *S. minuta*), and together they chase away predators (hen-harriers, etc.) from the colony. However, as regards the procuring of food, there is a sharp difference between them, for every species pursues a definite kind of animal in perfectly definite conditions. Thus the sandwich-tern flies out into the open sea to hunt certain species of fish. The blackbeak-tern feeds exclusively on land, and it can be met in the steppe at a great distance from the sea-shore, where it destroys locusts and lizards. The common-tern and the little-tern catch fish not far from the shore, sighting them while flying and then falling upon the water and plunging to a small depth. The light little-tern seizes the fish in shallow swampy places, whereas the common-tern hunts somewhat further from the shore. In this manner these four similar species of tern living side by side upon a single small island differ sharply in all their modes of feeding and procuring food.

(8) Another ecological notion is also important in connection with our experiments. We have in view the degree of isolation of the microcosm. The point is that our experimental researches have been mainly made in isolated microcosms, i.e., in test tubes filled with

nutritive medium and stopped with cotton-wool. It must be remembered that the degree of isolation of different communities in natural conditions is very different. Such a system as a lake is almost isolated, but at times some of the animals inhabiting it go on land. An oasis in the desert would also seem to be isolated, but for instance some of the species of birds fly away for the winter, and consequently there is no real isolation. The habitats not so sharply separated from the surrounding life-area are, therefore, still less isolated. All this emphasizes the idea already expressed, that the regularities observed in isolated microcosms hold true only under certain fixed conditions, and are not sufficient to explain all the complicated phenomena taking place in nature. We shall have an opportunity to appreciate the role of this factor when experimentally studying the predator-prey relations.

Let us note another important circumstance connected with competition. This phenomenon can be particularly pronounced during a periodical food shortage connected with certain seasons, etc., whilst at another time with an abundance of food it will scarcely take place. This fact has frequently been pointed out in various discussions of the struggle for existence.

(9) It remains but to give some examples of the struggle for existence among animals in order to show with what problems the zoologists have to deal, and how difficult it is to apply here exact quantitative methods. An instructive example of competition among fishes has been recently described by Kashkarov ('28). It concerns the supplanting of *Schizothorax intermedius* by wild carp, *Cyprinus albus* L., in lakes of Middle Asia. Wild carp were introduced into the lake Bijly Kul in 1909. Before that only *Schizothorax intermedius* with white-fish (*Leuciscus* sp.) inhabited this lake. Formerly *Schizothorax intermedius* were very numerous, but after the introduction of wild carp their quantity diminished considerably. As an indicator of the relatively small number of *Schizothorax intermedius* the following data on the catch may serve: on May 15, 1926, 19 carp and 1 *Schizothorax* were caught in two nets; on May 16, 1926, in the same place the catch was 24 carp and 2 *Schizothorax*. *Schizothorax* keeps chiefly to the south-western part of the lake, where there are stones making the casting of nets difficult. Now *Schizothorax* is disappearing even there, as wild carp devour its spawn. The quantity of whitefish also decreases because carp devour its young. The particular interest of this example lies in the fact that a new species not found in a given microcosm before (*Cyprinus albus* L.) was introduced, and in this way a direct proof of one species displacing another was obtained.

(10) Processes of this kind can often be observed when fish are introduced into waters to which they are new. Professor G. C. Embury writes in a letter recently received: "Concerning the competition

between different species of fishes we have two cases in particular in the eastern United States. The European carp was introduced in the '70's, and has now in many streams and lakes multiplied to such an extent that several native species are found in greatly diminished number. This has probably been due to the high reproductive capacity of the carp, food competition, destruction of weed beds by carp, and the fact that very few of them are captured.

Carp are not used as extensively for food in America as in Europe and in our smaller lakes are not generally fished for commercially. The other case is the introduction of the perch (*Perca flavescens*) into certain lakes in the Adirondacks and in Maine, which were naturally populated with the trout (*Salvelinus fontinalis*). The competition for food is believed to be one of the causes for the decrease in the number of the trout."

"These cases are both matters of general observation. I do not know of any papers describing them nor in fact, dealing with this subject in American waters."

(11) Another example of competition is the replacing of one species of cray-fish by another in certain waters of Middle Russia. Some observations on this were made by Kessler ('75) and recently by Birstein and Vinogradov ('34). Two species of cray-fish inhabit the waters of European Russia: the broad-legged (*Potamobius astacus* L.) and long-legged (*Potamobius leptodactylus* Esch.). The broad-legged cray-fish is distributed in the western part, and the long-legged in the south-eastern one, but the areas of their distribution largely overlap one another. It is observed that the long-legged cray-fish displaces the broad-legged one and spreads gradually more and more to the west. It has been possible to establish this replacement with particular distinctness in White Russia (in the western part of U. S. S. R.). The cray-fish are found there in lakes isolated from each other, and most of the lakes are inhabited only by the broad-legged cray-fish. In some cases long-legged cray-fish were put into such lakes from other waters. As a result the broad-legged cray-fish began to decrease, and *finally disappeared completely* leaving the lake populated exclusively by the long-legged species. The following examples can be given. (I) Black lake (White Russia) was populated only by the broad-legged cray-fish. In 1906, 500 specimens of long-legged cray-fish were introduced, and now (1930) only this species remains. (II) Forest lake (same region). Up to 1920 there were no long-legged cray-fish there. Later on they were introduced, and at present (1930) there is a considerable number of this species. The causes why one species of cray-fish is replaced by another have scarcely been studied.

(12) Curious are the observations reported by Goldman ('30) on the

competition among predators belonging to different species. Thus, according to a resident of Telegraph Creek near the Stikine River, Canada, no coyotes were known in that section prior to 1899. About that time, however, they came in, apparently following the old goldrush trail, probably attracted by the hundreds of dead horses along it. The invasion of Alaska seems destined to continue until coyotes have extended their range over practically all of the territory. It has been found in Alaska that the coyotes kill many foxes. Since the coyotes have increased the foxes have decreased alarmingly. In some sections practically none are believed to be left. In many cases a family or entire colony of foxes are run out of their dens or are both run out and killed by coyotes which then use the dens themselves. Wolves are well known to have committed similar depredations, but their killing is not so extensive as is that of the coyotes. Serious as are the depredations of wolves throughout most of Alaska, the damage done to game and fur bearing animals by coyotes is not only far greater but is rapidly increasing in extent. How far the coyotes will hold back the normal development in the periodical increase of the snowshoe rabbits and the ptarmigan which are important items in the food supply of fur bearers, especially the lynx and fox, it is impossible even to approximate.

(13) The examples just mentioned show that the introduction of aquatic animals into waters to which they are new, or the penetration of land animals into new regions, often lead to very interesting processes of competition. We would now like to say a few words about the *direct* struggle for existence, in which one species devours another. In this case it is very important to ascertain the exact numerical relation between the population of the devoured species and that of the devouring one, and this can often be attained by changing their relative quantities. One of the outstanding facts is the increase of the deer accompanying the destruction of wolves, foxes, etc., by early settlers in Illinois which, according to Wood, has been recently reported by Shelford ('31). Wood depicts a continuous decrease in wolves and wildcats from the beginning of settlement to their practical extinction. When the wolf population was reduced to about one half, the deer increased rapidly for a little less than 10 years, reaching a large maximum of about three times the original number. Unfortunately we have no *exact* data on the change of the numerical relations between the wolves and the deer, but such processes are in any case of great interest.

The change of the numerical relation between the predator and the prey sometimes takes place as a consequence of a mass appearance of the prey in years especially favorable for its multiplication. This frequently happens with wild mice, and it gives us the possibility of tracing the process of their being devoured by the predator. In this

connection we may mention the following observations recently made by Kalabuchov and Raewski ('33) in the North Caucasus: "The picture of the destruction of mice by different predators is a curious one. At the beginning of the destruction about the same number of rodents is devoured daily. But as the density of rodents diminishes it becomes more and more difficult to catch them, and the number of mice devoured gradually decreases. Finally a time comes when the relation between the density of the rodents, the presence of cover or refuge (burrows, vegetation, etc.) and the biological peculiarities of the predators becomes such that the latter can devour the rodents only in rare cases. In this way the number of the rodents remains about constant.

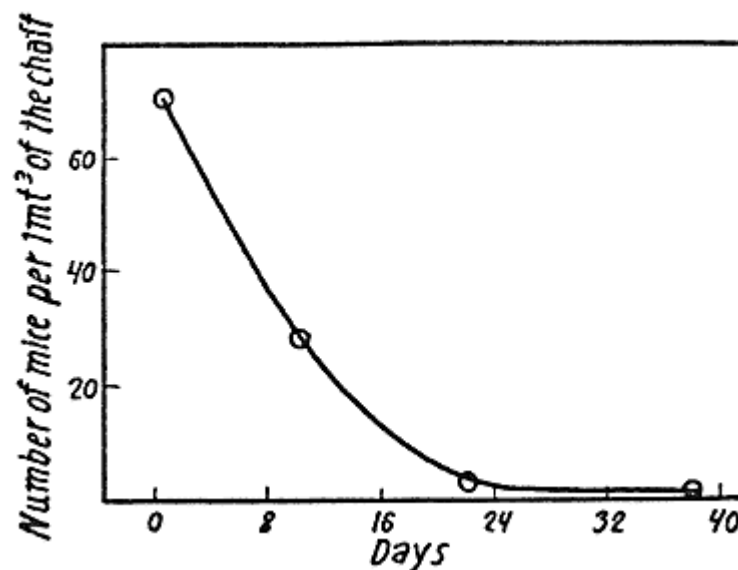


Fig. 2. The destruction of mice by different predators in heaps of chaff

"The data on the change in the number of mice near the village of Kambulat are a good illustration of this regularity. Having established that the destruction of mice in this locality was due to owls, polecats and other predators that devoured them, we obtained the following picture of the change in the number of the rodents in heaps of chaff (Fig. 2). This figure shows that with a density of 2.5-0.8 mice per m³ of chaff we have conditions in which the destruction of the rodents by the predators became so rare that their number scarcely varied."

Certain interesting observations have been also recently made by ecological entomologists (Payne, '33, '34) on the host-parasite balance. It is possible to trace the process of the destruction of population of the moth *Ephestia* by the hymenopterous parasite *Microbracon* in the laboratory, and it appears from the observations that a great many

factors are important for the process of their interaction, and particularly various relations between "susceptible" stage of host and "effective" stage of parasite. The beginning of the theoretical investigation of this case has been given by the interesting papers of Bailey ('31, '33) and Nikolson ('33). For such investigations, however, the populations of unicellular organisms are somewhat more convenient.

(14) The few examples given above show sufficiently that the processes of the struggle for existence among animals are of extreme importance from a practical point of view. They are sharply outlined in isolated microcosms and therefore there is nothing surprising if they have attracted the particular attention of the workers in the domain of fishery. Lately the problem of the relations between predatory and non-predatory fish has been discussed by Italian authors (D'Ancona ('26, '27), Marchi ('28, '29), Brunelli ('29)). D'Ancona collected the data of a statistical inspection of the fish markets in Triest, Venice and Fiume for several years. He claims that the diminished intensity of fishing during the war-period (1915-1920) has caused a comparative increase of the number of predatory fish. He therefore reasons that fishing of normal intensity causes a relative diminution of the number of predatory fish and a comparative increase of the non-predatory ones. But his data are not convincing and indeed Bodenheimer ('32) has recently shown that such variations in the fish population existed before and after the war. They are apparently not connected with the intensity of fishing but probably are the results of certain changes of the environment. However it may be, the material collected by D'Ancona stimulated the highly interesting mathematical researches on the struggle for existence of Vito Volterra. Although his mathematical theories are not confirmed in any way by D'Ancona's statistical data, the importance of Volterra's methods as a new and powerful tool in the analysis of biological populations admits of no doubt.

(15) In concluding this descriptive chapter of our book let us note the following picture of the struggle for existence in nature. It is only in the domain of botany that these processes are coming to be investigated from a certain general viewpoint as (1) intensity of competition, (2) competition in mixed populations, (3) the influence of environment upon competition in mixed cultures, and (4) the role of the quantitative relations between species at the beginning of their struggle. Among animals the processes of the struggle for existence are much more complex, and as yet one cannot speak of any general principles. In this connection an investigation of the elementary processes of the struggle for life in strictly controlled laboratory conditions is here particularly desirable, and the material just presented will be of great help to us in the choice and arrangement of the corresponding experiments.

