E.B. REED

Z 740

[1966]

D

24458
1893

The Biological Productivity of Waters[1,2,3]

By V. S. Ivlev

Institute of Hydrobiology
Ukrainian Academy of Sciences
Kiev, USSR

TRANSLATOR'S FOREWORD

The death of Viktor Sergeevich Ivlev on December 3, 1964, ended the career of one of the world's most active experimental scientists in the fishery field. Born at Tambov on August 6, 1907, Ivlev attended Moscow University, then worked successively at the Limnological Station of Kosino near Moscow, the Central Pond Fisheries Institute and Moscow Fisheries College, the Astrakhan National Park, the Institute of Hydrobiology of the Ukrainian Academy of Sciences in Kiev and Lvov, the Latvian Branch of the Central Institute for Lake and River Fisheries in Riga, and finally at the Sevastopol Biological Station of the Academy of Sciences of the USSR.

Whatever his surroundings, throughout this life Ivlev occupied himself principally with experimental studies on the physiology, nutrition, and behaviour of aquatic animals, both fishes and invertebrates. His best-known work is perhaps "Experimental ecology of the feeding of fishes," published in English in 1961 from the Russian original of 1955. However, even before the war Ivlev's experiments had attracted much attention both inside and outside the Soviet Union, while his versatility became very widely recognized following the appearance in 1945 of the review article "The biological productivity of waters." The latter work is still his major contribution to a synthesis of ecological and physiological information concerning aquatic production; and it is of topical interest today because of the impetus being given to studies in this field by the International Biological Program. A translation made at Indiana University in 1946 was not very widely distributed, so it is useful to have an English version made generally available in printed form.

The present translation is based on the 1946 version, but it has been completely rechecked against the Russian text. Some minor errors have been corrected, and numerous changes in wording have been made for clarity or euphony, or for greater faithfulness to the original. In addition, the paging of the Russian text has now been indicated, and also the Russian form of many technical terms — this last partly as an aid to further reading of the Soviet literature, partly because there is sometimes doubt concerning what is the best English equivalent. I have also added a few footnotes that may help to relate certain points to earlier and later work in this field; and an abstract has been prepared, in conformity with the policy of this Journal. All such additions are put in square brackets.

The Fisheries Research Board of Canada is publishing this translation as a memorial to a talented scientist, who was also a most engaging personality. An obituary written by two of his former colleagues, Ya. A. Birstein and G. R. Winberg, concludes as follows: "A connoisseur of art and literature, an amateur of sports, and a stimulating conversationalist, Ivlev continually astonished his friends by his unusual catholicity of taste, his lively interest in very diverse problems of culture, science and social life, and by his inexhaustible joie de vivre".

W. E. Ricker
June 15, 1966

ABSTRACT

[The concept of biological production is best approached from the point of view of a *product*, defined as a group of organisms (not necessarily all belonging to the same species) which have

---

[1] Received for publication March 24, 1966.

[2] Original title: Biologicheskaya produktivnost' vodoemov. Published in *Uspekhi Sovremennoi Biologii*, Vol. 19, No. 1, p. 98–120, 1945.

[3] Fisheries Research Board of Canada, Translation Series No. 394.

J. Fish. Res. Bd. Canada, 23(11), 1966.
Printed in Canada.

similar food habits, and which are useful to man or are of special interest for some other reason. *Production* is defined as the sum of all organic matter added to the stock of a product (or other defined organic unit) in a unit of time, regardless of whether or not it remains alive (i.e. part of the stock) at the end of that time. Production may be expressed in various units, particularly biomass (wet or dry weight), nitrogen content, or calorific content, but the last of these is to be preferred.

In order to trace the flow of energy in a body of water from solar radiation up to a given product, four types of study are needed. The first is a quantitative determination of the formation of primary organic matter — the fixation of solar energy by plankton and macrophytes. For plankton this is estimated from the oxygen produced (usually in light-and-dark-bottle experiments); for macrophytes, direct measurements of the growth of the plant body have been used.

Secondly, the paths of energy transformation that lead to the chosen product must be identified. Although a complete analysis for even one product would usually be extremely complex and tedious, the complexity can be greatly reduced by concentrating on the predominant foods of each organism and ignoring second-grade components.

Thirdly, the *ecotrophic coefficient* must be determined for each step in the food pyramid that leads from primary organic matter up to the product. The term ecotrophic coefficient is defined by Ivlev in two different ways. In discussing the flow of energy through an ecosystem, what is involved is the "dynamic" ecotrophic coefficient, the ratio of a consumer's intake of a particular food organism to the latter's production during some rather long time interval — usually a year. The energy content of the production of each food present, multiplied by the corresponding dynamic ecotrophic coefficient, gives the energy of that type ingested by the consuming organism during the time unit chosen; and the sum of these quantities for all foods eaten by this consumer gives the total energy that ascends that step in the food pyramid per unit time. Bacteria must of course be considered, both as consumers and as foods, and must be included in the picture whenever they comprise one of the steps leading to the chosen product. Unfortunately, measurements of the dynamic ecotrophic coefficient have scarcely begun; to be useful they must be carried out in real bodies of water, not in the laboratory.

What may be called the "static" ecotrophic coefficient is the ratio of the quantity of a particular food consumed to the total supply of it available at a given time; it is useful, for example, in studying daily rations. Laboratory experiments in this field have demonstrated a numerical relation between the quantity of food present and the quantity consumed, and also the fact that consumption increases if the food is distributed in aggregates.

Finally, there must be determinations of the *energy coefficient of growth* — the fraction of consumed food that is converted into body substance, for each step. This coefficient has very similar values (about 0.35) for the very young (but post-embryonic) stages of practically all animals, but it decreases with age and approaches zero as growth ceases; the course of this decline can be represented by a parabola. External factors, temperature in particular, have little effect on the magnitude of the growth coefficient. The production of any organism is equal to the quantity of food it ingests multiplied by the growth coefficient.]

1. The attempt at a theoretical generalization of the enormous factual material that has been accumulated in the course of studying the biological phenomena that occur in the water has produced two important trends in hydrobiology.

First in time, of these theoretical trends, was the scheme put forth by Thienemann and Naumann for the classification of lakes into "types."

Recent years have produced the second trend, which considerably surpasses the first both in the extent of the various biological processes it includes, and also simply in the complexity of its principles and in the differences of opinion that exist concerning it. In the pertinent literature this trend has been called

---

the problem of the bi
biological investigat
dynamic aspect of
consideration the fa
The necessity, in an
use of weapons from
siology, microbiolog
ceptions entertained
whole and also co
risky analogies with
importance of the
the need for a syste
has a bearing on th
of trying to indicate
problem in the futu
2. The concep
pond-fish culture w
in content. Numer
of pond-fish cultur
fish culturists unde
the average annual
This concept w
when he defined th
body of water to
product," and he u
product taken from
article Thienemann
production of orga
of the basic laws go
for quantitatively e
In 1932 Müns
discussion that is o
tivity. Ström's prop
If we imagine
and is absolutely s
actual productivity
produktivnost' pote
corresponding to th
zone of photosynth
liberated later from
stratum." Actual p
deducting the quan
In addition, Ström i
i valovaya produkt
result of productiv

the problem of the biological productivity of waters. In contrast to earlier hydrobiological investigations, it has as its goal the quantitative evaluation of the dynamic aspect of the biological processes in a body of water, taking into consideration the factors that determine the final result of this phenomenon. The necessity, in answering questions pertaining to this problem, of making use of weapons from an extensive arsenal of related disciplines (ecology, physiology, microbiology, hydrology, chemistry, and so on); the different conceptions entertained by different investigators concerning the problem as a whole and also concerning its individual parts; the broad and sometimes risky analogies with other biological phenomena; and finally the great practical importance of the problem in question — all these considerations indicate the need for a systemization of the already existing theoretical material that has a bearing on the problem of biological productivity, and the importance of trying to indicate the basic steps to be taken in any realistic study of this problem in the future.

2. The concept of biological productivity which came from practical pond-fish culture was originally completely concrete and purely practical in content. Numerous fishcultural investigations and the latest handbooks of pond-fish culture (Walter, 1928; Eleonsky, 1936; etc.) all indicate that fish culturists understand the productivity of a given body of water to be the average annual production of fish taken from it, expressed in weight units.

This concept was extended to natural waters by Thienemann (1931), when he defined the term *productivity* [produktivnost'] as the capacity of a body of water to produce a particular quantity of a "commercially-useful product," and he understood by *production* [produktsiya] the amount of this product taken from a unit area of the body of water in a unit of time. In this article Thienemann scarcely touches on the paths by which the process of production of organic matter is accomplished; he points out our ignorance of the basic laws governing the phenomenon, and also our ignorance of methods for quantitatively evaluating the dynamic side of the process.

In 1932 Münster-Ström published a paper which contains a detailed discussion that is of special significance [page 99] in connection with productivity. Ström's propositions may be summarized as follows:

If we imagine an "ideal body of water" which has an insoluble basin and is absolutely self-contained, then it is possible to distinguish between actual productivity and potential productivity [produktivnost' aktual'naya i produktivnost' potentsial'naya]. The latter term includes "the organic matter corresponding to the total amount of the 'minimal' salts which exist in the zone of photosynthesis, plus the total quantity of these salts which can be liberated later from the organic matter that exists at that time in the same stratum." Actual productivity will correspond to potential productivity after deducting the quantity of "minimal" salts in this same zone of photosynthesis. In addition, Ström introduces the concepts of net and gross production [chistaya i valovaya produktsiya], using the term production in general to mean the result of productive processes, i.e. the elaboration of organic matter from inorganic. Gross production is defined as the sum total of all organisms produced in a given interval of time, without regard to their later fate. Net production is the difference between the abundance of organisms at the initial and final moment of a period of time, and can be either positive or negative.

These concepts Ström carries over to "real" bodies of water, with certain modifications. For example, in changing to a "real" body of water, to the definition of potential productivity given above for an "ideal" body of water he adds "plus the organic matter corresponding to the net inflow of 'minimal' salts, plus the 'minimal' salts from decomposition of the organic matter that has entered during the period considered". Net production for real bodies of water "is a positive quantity, corresponding to the quantity of organic deposits on the bottom which are formed during the production processes and which are not returned to the food cycle, and the quantity of organisms that leave the lake in one way or another (outflow in rivers, emergence of insects, fishing)."

Ström's scheme, in spite of its elegance and a number of other unexceptionable qualities, nevertheless leaves much to be desired. The limitation of the concept of productivity solely to producers [photosynthesizing organisms], and the exclusion of all other organisms from consideration, restricts the problem too much. The single factor used by Ström — the quantity of organogenic salts — narrows the question greatly, even for producers. Very dubious too is his attempt to define the net production of a body of water as the sum total of the organic matter which escapes from the cycle [iz krugovorota]. As a result, Ström's scheme can more easily be applied to the problem of the balance of biogenic salts than to the problem of biological productivity of a body of water. Hence, it is no accident that in turning to actual, practical, natural conditions, the author himself strays from the strict logic of his previous reasoning and becomes inconsistent in the application of his concepts.

3. In 1936, in the pages of the "Zoologicheskii Zhurnal," there were published five articles on the question of productivity, which are of definite value in that they characterize the state of the problem as a whole.

The discussion was opened with an article by Brotskaya and Zenkevich (1936),[4] who point out, with complete justice, the deficiencies of Ström's system, and then give definitions of basic positions that are equivalent to the concepts proposed and formulated by Thienemann. These authors make use of three categories: productivity, production, and biomass [produktivnost', produktsiya, biomassa]. They write: "Under productivity (fertility [plodorodie]) we include the complete phenomenon as a whole, in all its varied aspects... the capacity of a body of water to maintain a particular type and rate of production of organic matter in the form of living organisms; hence we use the term 'productivity' [page 100] without reference to the time factor." "Production (crop [urozhai]) represents the increase of biomass in a given interval of time, which consists of (1) natural increase of the biomass as a result of growth, (2) the birth of new individuals, and (3) loss of biomass

---

[4] See also Brotskaya and Zenkevich (1939) and Zenkevich (1934).

---

resulting fr
production
of the proc
quantitativ
productive
such phen
peculiaritie
meropriyat
4. A
prerequisite
"since prod
By a produ
"Any of the
as can the
amount of
the existing
product"),
directly tra
the two ab
factor in p
tions invol
next step t
Winbe
two very u
and the cy
naya] proc
naya] prod
of time, m
myslovaya]
only to co
mainly wit
rectly prop
elements in
of heterotr
production
slight degr
connection
of organic
any accour
"We may
equivalent
meaning, s
If Wi
a considera
nig" — the

organisms pro-
r fate. Net pro-
s at the initial
ve or negative.
er, with certain
water, to the
body of water
w of 'minimal'
ic matter that
for real bodies
ity of organic
processes and
organisms that
nce of insects,

other unexcep-
The limitation
hesizing orga-
tion, restricts
e quantity of
oducers. Very
ody of water
cle [iz krugo-
o the problem
productivity
ual, practical,
f his previous
ncepts.
" there were
re of definite
le.
nd Zenkevich
s of Ström's
valent to the
uthors make
oduktivnost',
[plodorodie])
d aspects. . .
and rate of
ence we use
ime factor."
in a given
iomass as a
of biomass

---

resulting from the natural death of organisms. . . Thus, we use the term crop — production — in the literal and broad sense of the word — as the intensity of the process of reproduction and growth of organisms, expressed in some quantitative unit per unit of time." In addition, under "basic indexes of the productive properties of a body of water," the authors propose to consider such phenomena as the distribution of living organisms, their individual peculiarities, and even "a system of possible procedures" [sistema vozmozhnykh meropriyatii].

4. A different point of view is held by Karzinkin (1936). As a basic prerequisite he puts forth a clear and concrete definition of a "product," "since productivity is a concept that can exist only in relation to a product." By a product, then, Karzinkin means "the final phase of a given process. . . ." "Any of the organisms in a body of water can be considered under this heading, as can their derivatives." The author distinguishes *actual productivity* "the amount of material provided by the resources of a body of water which, under the existing conditions of the milieu, can be transformed directly into the product"), *potential productivity* ("hidden capacity, not capable of being directly transformed into the product"), and *gross productivity* (the sum of the two above). Regarding the trophic character of a body of water as a basic factor in productivity, Karzinkin deliberately narrows the problem "to questions involved in food production in bodies of water," and considered the next step to be a study of the system food → product.

Winberg (1936), in his treatment of the phenomenon, starts out from two very useful premises: the stability of the properties of bodies of water, and the cyclic character of productivity. He distinguishes primary [pervichnaya] production (Urproduktion of German authors), secondary [vtorichnaya] production (the increase of particular heterotrophic forms per unit of time, minus losses of any sort during the same period), commercial [promyslovaya] production or yield [ulov], and potential production (applicable only to commercial production). Following Ström's example, Winberg deals mainly with the basic primary production, which he postulates as being "directly proportional" [v pryamoi zavisimosti] to the abundance of organogenic elements in assimilable form. The general limiting condition for production of heterotrophic organisms is considered to be the magnitude of the primary production; which in reality, however, is commonly utilized to only a very slight degree — that is, there are other limiting factors. After analyzing the connection between the problem of productivity and questions of the balance of organic matter, and also giving a list of propositions on whose understanding any account of biological productivity must be based, Winberg concludes: "We may say that the above concept of productivity in the broad sense is equivalent to certain terms sometimes met with, which have no definite meaning, such as, for example, 'the dynamics of organic matter'".

If Winberg comes to the conclusion that biological productivity is to a considerable degree a synonym of an expression "having no definite meannig" — the dynamics of organic matter — pessimism of a different sort can be detected in the words of Muraveisky (1936). Beginning with the statement that "by the term biological productivity we mean the capacity of a body of water to produce organic matter in the form of living organisms," this author goes on to say that a theory of biological productivity [page 101] must solve such questions as, for example, the control of water blooms, the purification of water, its action on concrete, etc. Drawing a broad parallel between productivity and the fertility of soils, the author in the end confesses his inability to select a unit for productivity and, more generally, decides that it is impossible to make any quantitative evaluation of it.

Finally, in Skadovsky's (1937) article various questions of physiological adaptation are treated and the relation between the latter and the problem of productivity is pointed out.

5. Let us look now at two works that do not belong to the above mentioned discussion. Surveying the foundations of limnology as a science, Rossolimo (1934) proposes to dispense with the concept of productivity entirely, insofar as it has been included in the problem of the balance of matter and energy in a body of water. Observing that the concept of biological productivity "presents a series of insuperable difficulties in its theoretical basis," Rossolimo comes to the conclusion that "the only correct presentation of the question of biological productivity is to consider it from the point of view of the total dynamics of organic matter in a body of water." It is impossible to agree with Brotskaya and Zenkevich (1936), who consider that "the question raised by L. Rossolimo amounts only to the substitution of one term for another" and that "contemporary hydrobiology includes under hydrobiological productivity the very same subject matter as is included under 'balance' by Rossolimo."

Zhadin (1940) devotes a special chapter of his monograph on the fauna of rivers and reservoirs to the problem of productivity. This author selects the observed fact of the accumulation of organic matter as his point of departure. Zhadin writes: "The piling up [nakoplenie] of organic matter by organisms, which is the biological production of a body of water, is closely connected with processes of accumulation [akkumulyatsiya]. The quantitative extent and the qualitative nature of this piling up of organic matter is primarily a function of the species (or group) composition of the animal (and plant) population." And later on: Biological productivity is a function of accumulation and bioecological affluence [obespechennost']." May we recall that by "bioecological affluence" Zhadin means "the supply of animal (in some cases also plant) organisms existing in a body of water or in some part of it, these corresponding in their ecological nature to the existing conditions. . . . " We may observe that in the one instance Zhadin interprets productivity in Muraveisky's manner (total organic matter in the form of living organisms); in the other, he gives his approval to the diametrically opposite point of view of Karzinkin, which regards the "product" as the starting point of the problem. In addition he adopts the division of production into "primary" and "secondary," in agreement with Winberg's views. Finally, adducing various examples

ı the statement
city of a body
rganisms," this
page 101] must
ɔms, the purifi-
arallel between
d confesses his
y, decides that

ɔf physiological
ıd the problem

ɔove mentioned
ıce, Rossolimo
ntirely, insofar
ter and energy
ıl productivity
basis," Rosso-
of the question
ew of the total
ssible to agree
"the question
one term for
r hydrobiolog-
ınder 'balance'

ı on the fauna
author selects
is point of de-
nic matter by
ıter, is closely
ıe quantitative
ter is primarily
al (and plant)
ɔn of accumu-
recall that by
(in some cases
art of it, these
ons. . . . " We
ivity in Mura-
ɔrganisms); in
point of view
ɔf the problem.
" and "secon-
rious examples

---

of the relation of productivity to accumulation and "affluence," the author substitutes for "productivity" the idea of richness [bogatstvo] of the population, that is, its biomass and species diversity.

6. The works cited are far from exhausting the examples of differences of interpretation of the question of biological productivity in bodies of water. The manipulation of abstract constructions, and the absence of efforts to put a concrete biological content into their structure, leads to a multiplication of such schemes, to the detriment of positive study of the problem. Furthermore, when these authors are engaged in the concrete solution of definite problems (for example, Winberg's study of photosynthetic processes or Karzinkin's work on the food and feeding of fishes) they move far from their respective general ideas.

In addition, it is typical to find that papers dealing with aquatic productivity are overburdened [page 102] with material that has no direct relation to that phenomenon. Without denying at all the obvious proposition that in a body of water all processes are to a greater or less extent interdependent, it seems to me that this does not provide any excuse, in speaking about productivity, for entering into a polemic about the typology of lakes, about the content of "hydrobiology" and of "biohydrology," and so forth and so on.

7. Recent years have produced still another trend in the question of the study of biological production of a body of water, the development of which is an accomplishment of American investigators. Great importance is attached to the problem of productivity in American literature, and it is not by accident that Welch (1935) emphasizes that the basic problem of limnology as a whole is the study of biological productivity.

The works of American authors, although they suffer from a certain vagueness in respect to questions of principles, are at the same time distinguished by concreteness and by an aspiration to bring under a general formulation the actual complex of data accumulated in the course of studying natural environments. Especially valuable in this respect are the numerous investigations carried out by the Wisconsin school, which provide as yet unsurpassed factual material on different aspects of the life-activities in a body of water. In recent years Juday, the leader of the school, has made an attempt at synthesizing the data obtained in a completely objective numerical calculation of the fundamental steps in the production process (Juday, 1940).

Special attention must be given to the school of Hutchinson (1942), who with coworkers has given, in my opinion, the most finished exposition of biological productivity. I must point out that my account of the theses of this school is taken from the work of Lindeman (1942), inasmuch as the principal summary by Hutchinson has remained inaccessible to me up to now: Lindeman, who presents extensive citations from it, refers to it as a manuscript.

8. In this context the concept of productivity begins with its formulation by Riley (1940) as the general rate of reproduction, and it can apply to any food group of an ecosystem; thus, productivity is considered as the quantitative

evaluation of the basic process of trophic ecology. We may note that the concept of an ecosystem (Tansley, 1935) is used by Lindeman as a point of departure in constructing his theory of dynamic ecology.

The particular attention of this school is centered on the question of the energy transformations in the flow of organic matter from one state to another in the food chain, or as Lindeman puts it, the transfer of energy from one part of the ecosystem to another. The stocks of organic matter accumulated in the process of photosynthesis constitute the original source of available energy, which stocks are subsequently used by the heterotrophic organisms belonging to the various trophic levels and which, in Thienemann's (1926) terminology, are consumers [organizmy-konsumenty]. Hutchinson gives the following mathematical interpretation of his position. As a result of photosynthesis solar radiation (Λ_0) is partly transformed into the organic matter of the bodies of plants (Λ_1 – the first level), which then is partly consumed by plant-eating animals (Λ_2 – the stock of energy at the second level), which in its turn serves as food for carnivores (Λ_3 – the third level). This series can be extended. It is obvious that the stock of energy at the different levels will not be the same, and will be the less, the higher the serial position of any level. Considering any level (Λ_n) of the food cycle, we see that its magnitude is the result of two opposed processes: the accession of energy from the previous level (λ_{n-1}), and release of energy to the next level (λ_{n+1}). [page 103] Consequently, the rate of change of the stock of energy at a given level will be expressed by:

$$\frac{d\Lambda_n}{dt} = \lambda_n - \lambda_{n'}$$

where λ_n is the rate of extraction of energy[5] from the previous level (a positive quantity), and $\lambda_{n'}$ is the rate of loss of energy to the next level (a negative quantity). Hence the quantity λ_n is also the true productivity of level n.

Hutchinson also introduces the concept of the efficiency of productivity of a given level (Λ_n) in relation to the productivity of any previous level (Λ_m), expressed quantitatively as the ratio λ_n/λ_m. As a basis of comparison we may use the solar energy (λ_0), but, as Lindeman observes, greatest interest attaches to ratios of the type λ_n/λ_{n-1}, i.e. a comparison of the rate of accession of energy by two adjacent levels.

A considerable part of Lindeman's paper is devoted to an analysis of the last-mentioned process, i.e. listing the factors that account for the loss of energy as it is transferred from one level to another, with an attempt at their quantitative evaluation. The author mentions three kinds of dissipation of energy during transfer to a higher level: expenditure in respiration; loss involved in predation, which boils down to the question of assimilability; and decomposition after death. Special importance is attached to the loss

---

[5] ["Skorost' otdachi energii"; λ_n evidently refers not to the rate of total energy consumption from level Λ_{n-1}, but rather to that part of it which is used for growth by Λ_n. On the other hand, $\lambda_{n'}$ must be the gross rate of consumption of Λ_n by Λ_{n+1}.]

---

in respirat
energy do
channel.
9. I
stocks of f
to formula
involved
biomass
the forma
unit of ti
a given q
the terms
from the l
evaluation
ration onl
trophic p
associated
cepts of t
only in t
and that
trophic gr
the increa
that is th
it is obvio
per unit
expressio
cyclical
also, as a
It se
tivity."
state of a
tion requ
apply onl
began. T
can be re
of water
to distin
as Ström
complica
study.
10.
troduces
of the p
evaluate
units of

ay note that the
eman as a point

e question of the
e state to another
energy from one
tter accumulated
urce of available
rophic organisms
nemann's (1926)
hinson gives the
result of photo-
e organic matter
partly consumed
nd level), which
. This series can
different levels
l position of any
at its magnitude
rom the previous
page 103] Conse-
level will be ex-

level (a positive
vel (a negative
of level n.
of productivity
vious level (Λ_m),
parison we may
nterest attaches
ession of energy

analysis of the
for the loss of
ttempt at their
of dissipation
espiration; loss
assimilability;
ed to the loss

ergy consumption
On the other hand,

---

in respiration, inasmuch as in predation and decomposition after death the energy does not escape from the food cycle, but merely falls into another channel.

9. In making observations on the process of consumption of natural stocks of food by fish in a body of water I have already taken the opportunity to formulate briefly my opinions concerning the fundamental considerations involved (Ivlev, 1939). I decided that it is advisable to use three concepts: biomass (in the sense of Demoll); production, including under that head the formation [vykhod] of new biomass by a given group of organisms in a unit of time; and productivity — the capacity of a body of water to produce a given quantity of organic matter in some particular form. Thus, I adopt the terms proposed by Thienemann and Zenkevich, and in so doing I depart from the latter's definition in only one respect, namely that in the quantitative evaluation of the productive capacity of a body of water I take into consideration only a single category of organisms, which are all alike in respect to their trophic processes. Such a group will meet the requirements that Karzinkin associated with the term "product," and will coincide exactly with the concepts of the American investigators. The definitions I propose differ from theirs only in the fact that my "production" corresponds to their "productivity," and that in Riley's work it is necessary to speak of the rate of *growth* of any trophic group of organisms rather than their "rate of reproduction"; for it is not the increase in numbers of organisms, but the increase in their total biomass that is the important element in the production process. On the other hand it is obvious that "rate of growth of biomass" and "formation of new biomass per unit of time" are synonyms; and if I do not favour using the more general expression "rate" of growth [skorost' rosta], that is solely because of the cyclical nature of the process of production, when the "unit of time" will also, as a rule, be the time of a natural cycle — one year.

It seems to me inadvisable to introduce the concept "potential productivity." Inasmuch as productivity is a reflexion [page 104] of the existing state of a body of water, the discussion of potential possibilities, whose realization requires a change in the body of water, is for that reason abstract and will apply only to a topographic entity different from that with which the discussion began. The existence of "primary" and the other similar types of productivities can be recognized without argument, in my opinion, inasmuch as in any body of water we can in general distinguish as many "productivities" as it is possible to distinguish groups of organisms that are trophically uniform. However, as Ström's scheme clearly illustrates, the introduction of other concepts merely complicates the question, without providing anything new to assist in its study.

10. In my opinion, application of the concepts enumerated above introduces clarity and precision into our understanding of the fundamentals of the problem. In the first place, it becomes quite obvious how we should evaluate the production process quantitatively, namely by expressing it in units of production of the organisms under consideration. Secondly, inasmuch

as in such an evaluation it is essential to select categories of organisms uniform as regards their position in the trophic relationships that exist in the body of water, the danger that Ström and Winberg feared disappears — that of "including one and the same organic matter twice over" in the course of its transfer from one state to another. There is no question that this last danger is a real one, because a number of authors understand by productivity the "sum" of the organic matter elaborated by and contained in organisms having very different positions in the trophic system.

Finally, there is something which I have not only taken into consideration in my work, but have regarded as one of the most distinctive characteristics of aquatic production processes — namely the participation of groups of organisms having different trophic characteristics, from green producers up to animal predators. This circumstance, the multiphasal nature [mnogofaznost'] of the aquatic production process, where heterotrophic organisms take part, sharply distinguishes this phenomenon from such concepts as fertility [plodorodie], crop [urozhai], yield potential [urozhainost'] and other phenomena of agronomy. However, the impossibility of transferring agronomical concepts directly to problems of aquatic productivity has an even more fundamental basis. It not infrequently happens that by hydrobiological productivity is meant a property *of the body of water*, considered as of a kind of microcosm; whereas in agronomy urozhainost' means the desirable features which are inherent *in a given type of management*, and which are realized in the form of the crop [urozhai]. The latter is not an absolute quantity; it is not [entirely] the result of the "urozhainost'" of the particular system of management, for it is affected by unfavourable factors of the external surroundings (Atstsi, 1932, etc.). I have dwelt on this matter at length because the analogy between the term "produktivnost'" and the agricultural "urozhainost'" has been widely used.

11. Looking on the phenomenon of productivity, in full conformity with the views of Hutchinson, as an energy process, it becomes desirable to consider some salient problems whose solution will make it possible to understand the phenomenon both in its general aspect, and in relation to concrete natural objects.

It is obvious that for the source of energy in waters, as elsewhere on our planet, we must look to the sun's radiation, transformed by photosynthesis into primary [iskhodnoe] organic matter. The formation of organic matter by means other than the activity of chlorophyll-bearing plants, although it is of wide enough occurrence in nature, is quantitatively inconsiderable in magnitude in comparison with the phenomenon of photosynthesis. In addition, autotrophic chemosynthesizing organisms, with a few exceptions (for example iron-bacteria), use as a source [page 105] of energy-providing material products that were formed by biological processes (hydrogen, methane, hydrogen sulphide, etc.).

As a rule primary organic matter first undergoes a series of biochemical transformations in the plant body itself, then it passes through various stages

---

in a subsequent
answering ques
must be to rev
from the prima
trate the steps i
formation are a

Up to this
by Hutchinson
not, in all its e
It is easy to re
given by Linde
occur in compl
each level can
one, or at a jun
include a consi
sense (for exam
lism" of organi
as Lindeman h
within a given

A picture
manner suited
system, taking
involved in tra
different popul
real identity in

12. It is
with each step

In the tra
reasons for inc
the former. Fi
that is, not all
Dispersion of
natural mortal
esses, spatial t
in nature, whe
away from th
the third requ
will be a det
describe the
another.

Finally, n
predator → pr
only some fra
rable, is in its
the organism

s uniform
the body
— that of
urse of its
ast danger
tivity the
ms having

nsideration
racteristics
groups of
producers
re [mnogo-
organisms
as fertility
phenomena
al concepts
undamental
luctivity is
microcosm;
which are
the form of
ot [entirely]
nanagement,
ings*(Atstsi,
ogy between
been widely

conformity
nes desirable
possible to
relation to

where on our
otosynthesis
ganic matter
although it is
ble in magni-
In addition,
(for example
erial products
ne, hydrogen

f biochemical
various stages

---

in a subsequent series of heterotrophic forms. Hence, the second step, after answering questions concerning the origin of the primary organic matter, must be to reveal the routes by which this migration of energy takes place, from the primary form up to the "product" that interests us, and to demonstrate the steps in the trophic cycles with which these processes of energy transformation are associated.

Up to this point our discussion does not differ from the position set forth by Hutchinson. However, Hutchinson's principle of "trophic·levels" does not, in all its endearing simplicity, correspond to the state of affairs in nature. It is easy to realize this if we consider the scheme of the dynamics of matter given by Lindeman in the form of a diagram, where different trophic levels occur in complex interrelationship with one another, so that the energy at each level can have proceeded either by a "legal" path from the previous one, or at a jump from a more distant one. Moreover, inasmuch as these levels include a considerable number of forms of very different sorts in the trophic sense (for example, the "level" zoobenthos), examples of a sort of "cannibalism" of organisms on the same level are possible and in fact not uncommon, as Lindeman has shown; that is, development of trophic structure occurs even within a given level.

A picture of the paths of energy transformation must be constructed in a manner suited to the body of water under consideration — to the whole ecosystem, taking account of the trophic characteristics of the forms actually involved in transporting the energy. Hence, lumping different species, or even different populations, into wider categories must be done only when there is real identity in respect to their food relationships.

12. It is obvious also there is inevitably a partial loss of energy associated with each step on the path of energy transformation.

In the transfer of energy from prey to predator there are two possible reasons for incomplete utilization of the energy contained in the biomass of the former. Firstly, it is not likely that all the individuals of the prey species, that is, not all their edible matter, will serve as food for the predator in question. Dispersion of energy to other trophic cycles (consumption by other organisms, natural mortality with consequent freeing of energy for microbiological processes, spatial transfer, and so on) can lead to a situation that frequently occurs in nature, wherein a great part of the energy is dissipated into side channels away from the special route which leads to the chosen "product." Hence, the third requirement for an objective evaluation of the production process will be a determination of the patterns and laws [zakonomernosti] which describe the quantitative aspects of the consumption of one organism by another.

Finally, not all of the energy consumed by the second stage in the system predator → prey is transferred to the body of the organisms concerned, but only some fraction of it; the other fraction, which is sometimes very considerable, is in its turn partly not assimilated, and partly diverted to maintaining the organism (so that it does not take part in the process of growth). For the latter kind of energy loss Lindeman proposes to introduce an appropriate correction; however, he fails to take into account the other type of energy loss described above (though this is perhaps not absolutely necessary when he is dealing with a concept of trophic levels that do not actually exist in nature).

Consequently, a realistic evaluation of production processes in a body of water must be based on knowledge of four features: (1) the process of synthesis of the primary organic matter; (2) the paths of transformation [page 106] of the latter into the final "product"; (3) the loss of energy resulting from failure to utilize all of the edible organisms present in each trophic step of the type consumer → food; and (4) loss of the energy in the matter ingested, and the degree of utilization of the latter for growth processes.

Let us try to set forth briefly the present state of progress in the study of these four processes.

13. Accepting the fact that the photosynthetic process of production of organic matter so greatly exceeds the chemosynthetic that the latter can be ignored in the study of aquatic productivity, let us consider the basic features of the study of the phenomenon of photosynthesis from that point of view.

In the water the role of producers can be played by plants of two categories: (1) phytoplankton; and (2) plants more or less closely associated with the substrate, of the type of the great marine algae and freshwater macrophytes, that is, the plants frequently classed as phytobenthos.

In bodies of water of different types these two groups can differ in their relative importance; however, for an overwhelming number of basins the dominant role is undoubtedly played by the phytoplankton.

At the present time methods exist for studying the photosynthesis of phytoplankton, the results obtained being expressed in units of organic matter (generally in the form of glucose) or, by using an oxycalorific coefficient, in energy units (Ivlev, 1934). The first method: two bottles, one transparent and the other impervious to light, are filled with water and the algae which it contains, and are lowered into a body of water to the level from which the water used to fill the bottles was drawn, i.e. to the same temperature and light conditions as the given complex of plankton forms lived in under natural conditions. After a certain time (usually about 24 hr) the oxygen content in the bottles is determined. The difference between the transparent and the opaque bottle provides a measure of the intensity of photosynthesis, while the difference between the original oxygen content and that of the opaque bottle gives a measure of the rate of decomposition of the organic matter. This method has been widely used for determining the vertical distribution of photosynthetic activity in relation to illumination (Ruttner, 1926; Marshall and Orr, 1928; Jenkin, 1930; Ehrke, 1931; and many later workers: Schomer, 1934; Juday and Schomer, 1935; Clarke and Oster, 1934). It was first described by Pütter (1924) as a means of evaluating the production process for plankton algae, although Pütter exposed his jars to light without lowering them to the appropriate level in the water. The same method was used by Gaarder and Gran (1927), Gran (1927, 1929, 1930) and Gran and Birgithe (1926),

---

who sank th
Maucha (192
production p
given the met
and from the
number of bo
very interesti
transformatio
method (Ivle
related to the

A transiti
the intensity o
of water dark l
between the b

[page 107
who first gave
used by Bruev

The basic
of oxygen in t
the light part
thetic activity
oxygen consun
the dark hours
slowness of the
and vice versa
place even on b
of special expe
the assumption

14. Thus,
matter by the
precise formula
varied waters,
open expanse of
large oligotroph
study of the p
is the sole agent

However, a
sea, not to men
and all small wa
of organic matte

Estimation
rently be carrie
weed from a sa
can be illustrate
perennial hold-f

ppropriate cor-
of energy loss
ary when he is
xist in nature).
sses in a body
process of syn-
tion [page 106]
resulting from
hic step of the
atter ingested,

s in the study

of production
e latter can be
basic features
nt of view.
s of two cate-
ssociated with
macrophytes,

differ in their
of basins the

osynthesis of
rganic matter
ic coefficient,
e transparent
algae which
m which the
perature and
nder natural
ygen content
rent and the
thesis, while
the opaque
anic matter.
distribution
26; Marshall
rs: Schomer,
rst described
for plankton
ng them to
by Gaarder
ithe (1926),

---

who sank their bottles into the sea for a considerable period; and also by Maucha (1924), who has fully tested the method as a means of answering production problems. Finally, Winberg (1934, 1936, 1937, 1937a, 1939) has given the method its contemporary form, both in its purely technical aspects and from the theoretical point of view. He also tried it out on a considerable number of bodies of fresh water of diverse character, from which he obtained very interesting data concerning the various aspects of the formation and transformation of organic matter in the water. A direct verification of the method (Ivlev, 1939) demonstrated its excellent applicability to problems related to the increase of organic matter in a body of water.

A transition to the second method is found in the technique of calculating the intensity of photosynthesis used by Heinrich (1934), who placed in a body of water dark bottles only, and considered that the difference in oxygen content between the bottles and the water mass was the result of photosynthesis.

[page 107] This second method also is linked with the name of Pütter, who first gave a description of it in the publication cited above. Later it was used by Bruevich (1936) and Winberg (1939), with certain modifications.

The basic factor that makes this method feasible is the daily dynamics of oxygen in the water mass: the accumulation of oxygen in the water during the light part of the 24-hr day is considered to be the result of the photosynthetic activity of the phytoplankton, while a correction for the process of oxygen consumption is obtained from observations on its decrease during the dark hours of night. The prerequisites for this method are, firstly, extreme slowness of the processes of diffusion of oxygen from the air to the water mass, and vice versa; secondly, the assumption that photosynthesis does not take place even on bright moonlit nights. The latter condition was made the subject of special experiments (Ivlev and Mukharevskaya, 1940), which showed that the assumption is correct.

14. Thus, the methods of determining rate of manufacture of organic matter by the photosynthetic activity of phytoplankton have received rather precise formulation and testing by a large number of investigators in extremely varied waters, from the ocean down to the ponds used in fish culture. In the open expanse of the ocean (excluding such special cases as the Sargasso Sea) or of large oligotrophic lakes, the methods described complete the first stage of the study of the production process, for under these conditions phytoplankton is the sole agent transforming solar energy.

However, as Petersen (1926) shows, even for the shoreward parts of the sea, not to mention shallow eutrophic lakes having a well-developed littoral, and all small waters, the predominant position as regards intensity of production of organic matter is taken over by phytobenthos.

Estimation of the production process for marine phytobenthos can apparently be carried out directly, with sufficient accuracy, by collecting the seaweed from a sampling station at a definite time of year. Such marine plants can be illustrated by forms of the type of *Laminaria* with annual leaves and perennial hold-fasts, and forms of the type of *Fucus* which are true perennials.

The first type is characterized by the fact that the plant body is a structure consisting of hold-fast and foliage, of which the first grows extremely slowly or for practical purposes remains unchanged during the course of a year, while the foliage drops off in winter or spring and a new one grows in its place. Under polar conditions assimilation [assimilyatsiya] usually ceases in winter among seaweeds, and only with the rise in assimilation in mid January does growth of young leaves begin (Smirnov, 1924). In more southern regions growth begins earlier — starting in mid December along the Norwegian coast (Printz, 1926), or in November along the shores of Sweden (Kylin, 1916); but in any event a time comes in summer when the seaweeds have attained their maximum growth. In the investigation of the Murman *Laminariae* by Kireeva and Shchapova (1938), this time was the interval immediately following the end of the process of sporulation. Afterward growth ceases, and the biomass of the algae begins to decline.

Among perennial seaweeds there is no complete loss of the foliage grown in the previous year, but nevertheless it is possible to distinguish the growth of the current year from that of previous years. Consequently, even for these forms a method of evaluating directly the intensity of the production process is available. [page 108] This method is quite reliable, as is shown in the above mentioned work of Kireeva and Shchapova for the *Laminariae* of the Murman coast, and by one Morozova-Vodyanitskaya (1936) for the algae of the Black Sea.

These methods of determining quantitatively the production of vegetable biomass have also found wide application with freshwater macrophytes. We may refer to articles by Rickett (1920, 1922, 1924); to some unpublished work by Borutsky on the production of various water plants which includes a careful consideration of all related factors (for example, death of separate parts of the plant in the course of the vegetative period); and to the summary by A. and N. Lipin (1935), which uses data collected by these authors as well as materials from other investigators. However, a serious difficulty arises here, which makes it a rather complicated matter to achieve reliable results. The difficulty consists in the fact that among many species of water plants there are stout perennial rootstocks that accumulate a considerable percentage of the organic matter produced. According to the Lipins' data, these rootstocks can exceed the erect parts of the plant by 2.5 times in the case of reeds [trostniki — *Phragmites*], or by as much as 5 times in cat-tails [rogozy — *Typha*]. Thus, in calculating the production of certain macrophytes on the basis of experimental cropping we run up against two unknown quantities: growth resulting from the reserve of organic matter stored up in previous years, and deposition of newly synthesized matter in the same rootstock system.

To escape from this difficulty we can make use of the principle stated earlier, that is, use a determination of the energy of photosynthesis throughout the whole vegetative period as a criterion of the intensity of productive processes. As far as I know, such experiments have not been carried out up to the present; however, the fact that methods of studying photosynthesis have

---

been devel
also for sul
For examp
respiration
(cited by B
15. T
organically
rounding m
of many of
plants, neve
may occur
for growth
The rel
can be cons
A numl
of organic n
at the start
the vegetat
phosphorus
Seiwell, 193
Cooper; Mo
Conside
cyclical nat
enter into o
109] again f
regarded as
in a given p
Greater
of biogenic
that in a situ
introduction
of the inten
hundred per
oyster banks
and also und
1939) and nit
object was th
salts can exe
of cells (Thir
formation du
necessary for
Finally,
of mineral n
and mixed cu
salt to natura

is a structure con-
extremely slowly
course of a year,
grows in its place.
ceases in winter
nid January does
southern regions
the Norwegian
Sweden (Kylin,
e seaweeds have
Murman *Lami-*
e interval imme-
fterward growth

he foliage grown
ish the growth of
, even for these
oduction process
wn in the above
e of the Murman
he algae of the

tion of vegetable
acrophytes. We
me unpublished
which includes
eath of separate
to the summary
authors as well
culty arises here,
ble results. The
ter plants there
e percentage of
these rootstocks
of reeds [trost-
gozy — *Typha*].
on the basis of
ntities: growth
ious years, and
ystem.
principle stated
esis throughout
productive pro-
rried out up to
synthesis have

---

been developed both for the aerial parts of plants (Lyubimenko, 1935) and also for submersed parts (Ruttner, 1926) suggests that this is quite practical. For example, Heinicke and Childers kept track of the photosynthesis and respiration of an entire young apple tree, in fruit, for a period of 6 months (cited by Brilliant, 1943).

15. The elaboration of organic matter by photosynthetic processes is organically linked to the presence of certain chemical elements in the surrounding medium. Although water ordinarily contains an adequate quantity of many of the elements necessary for the synthesis of the organic parts of plants, nevertheless, some of these elements, which have been called "biogenic," may occur in insufficient concentrations, thus limiting the potential capacity for growth of the plant biomass.

The relation of mineral nutrients to the problem of aquatic productivity can be considered in different ways.

A number of investigators have made an attempt to estimate the quantity of organic matter produced, on the basis of the abundance of certain elements at the start of the vegetative growth of plankton (in winter) and at the end of the vegetative period (in autumn). The following elements have been used: phosphorus (Atkins, 1926; Kreps and Verjbinskaja, 1932; Cooper, 1933; Seiwell, 1934, 1935), silicon (Cooper), nitrogen (Cooper), carbon (Atkins; Cooper; Moore et al., 1915).

Considering the multiphasality of production processes and also their cyclical nature, when one and the same quantity of biogenic substance can enter into organic combinations and then, after the latter decompose [page 109] again fall into solution, these efforts cannot be considered successful if regarded as objective evaluations of the quantity of organic matter created in a given period of time.

Greater interest attaches to the few works devoted to the direct effect of biogenic substances on the process of photosynthesis. It has been shown that in a situation where a particular plant exhibits a need for a certain element, introduction of the same into the water results very quickly in an increase of the intensity of photosynthesis, which increase may amount to several hundred per cent. This has been demonstrated under natural conditions on oyster banks (Gaarder, 1932), in respect to phosphorus and nitrate nitrogen, and also under experimental conditions in respect to potassium (Pirson, 1937, 1939) and nitrogen (Van Hille, 1938). In both the latter studies the experimental object was the freshwater alga *Chlorella*. To the above we may add that mineral salts can exert an influence also by way of stimulating an increase in the size of cells (Thimann and Schneider, 1938), and in addition we may point to the formation during the process of photosynthesis of certain unknown substances necessary for the process of cell division (Karsten, 1918).

Finally, wide publicity has been given to methods for evaluating the effect of mineral nutrients on the process of growth of algal populations in pure and mixed cultures. The essence of this method consists in adding some nutrient salt to natural water with its accompanying culture of algae; after the lapse of a certain time, on the basis of the intensity of growth of the culture, conclusions are drawn as to whether the quantity of this element in the water used is inadequate or is present in excess, for the algae in question. Schreiber (1927) was the discoverer of this method of "evaluation of hydrobiological reproductivity" [vosproizvoditel'nost']; however, it was brought to full development by Frantsev (1932) and Guseva (1938) with the idea of predicting the onset of algal blooms in reservoirs. I believe that the Schreiber–Frantsev method must play a very important role when applied to problems concerned with the study of mineral nutrients of algae, as one aspect of the problem of productivity, since it allows us not only to decide what quantity of a given element is necessary but even the type of compound in which it must be present; for different species of water plants react sensitively to the form in which a particular element occurs. For example, nitrogen for one species must be in the nitrate form; for another, as nitrite, for a third, in the form of ammonium compounds (oral communication of Frantsev). This method offers special opportunities for quantitative analysis of the phenomenon, by applying the scheme of Mitscherlich (1925) either in its original form or with suitable modifications (Kirsanov, 1930).

We may observe that the biogenic substances dissolved in the water will also govern the growth of water macrophytes and of course marine algae as well, for it is known (Gessner, 1933) that for the majority of water plants the root system is not an organ that extracts mineral salts, these being absorbed directly from the water round about.

A characteristic of the extensive literature on the fertilization of fish ponds is that it is extremely uneven in quality and is composed of a multitude of statements and facts of very varied content (Demoll, 1925). The reason for this is to be found in the inadequate consideration given to the methods of presentation used, which lack any attempt at a comprehensive analysis of the complex mechanism of energy transformation in the waters concerned.

16. Closely associated with the problem of elaboration of organic matter, and with the role of mineral nutrients in this process, is the phenomenon of disintegration [raspad] of this newly-formed organic matter. [page 110] This phenomenon has a two-fold importance for the problem before us: in the first place, as a result of the disintegrative process a part of the energy supply is used up without getting into any subsequent stage of transformation; in the second place, this process results in the formation and release into the water mass, or into the soil at the bottom of the body of water, of a certain quantity of biogenic elements capable of entering a new cycle.

Disintegration of the organic matter of the producers can take place either by way of catabolic processes or as decay following death.

Study of processes of the first type leads to a purely physiological determination of the intensity of respiration. Experiments have shown that carbohydrates are the actual materials used up by plants in respiration (Kostychev, 1937), i.e. substances which are in the first stages of synthesis and which have not achieved further energy transformation. On the other hand, Pütter and

more recently R
stances to the s
unassimilated p
showed that alg
stances which h
transformation.
the production
which part of th

The proces
place on a scal
very different t
reduction [redu
decomposition
An essential fe
purely chemica
and all "decon
ganisms (Kuzn
rushenie] of org
far beyond the
man and Care

17. Earli
us to make use
diverse in thei
understanding
of water, from
becomes the s

The path
of food intern
for selected s
themselves or
that interest
nutrition of t

In these
in a "vertical
done, into gr
groups.

The imp
complex. Ac
who unlike o
algae, then t
representing
is the more
group — the

Howeve
from the ter

h of the culture, con-
element in the water
in question. Schreiber
on of hydrobiological
was brought to full
the idea of predicting
e Schreiber–Frantsev
o problems concerned
ect of the problem of
quantity of a given
ch it must be present;
the form in which a
e species must be in
e form of ammonium
nethod offers special
on, by applying the
r with suitable modi-

ved in the water will
urse marine algae as
rity of water plants
these being absorbed

fertilization of fish
posed of a multitude
, 1925). The reason
iven to the methods
prehensive analysis
e waters concerned.
n of organic matter,
the phenomenon of
ter. [page 110] This
before us: in the
f the energy supply
transformation; in
nd release into the
water, of a certain
cle.
an take place either

physiological deter-
ve shown that car-
iration (Kostychev,
esis and which have
hand, Pütter and

---

more recently Rohberg (1930) have demonstrated the release of organic substances to the surrounding medium, and consider that these substances are unassimilated products of photosynthesis. However, Aleev (1934, 1936) showed that algae in suspension give off nitrogen compounds also, i.e. substances which have already travelled along the intricate path of biochemical transformation. This latter circumstance has to be considered in calculating the production of organic matter by plants, for they are one of the outlets by which part of the energy is lost to the rest of the cycle.

The process of decomposition after death [posmertnoe razlozhenie] takes place on a scale incomparably greater than the above. We may observe that very different terms are in use for the disintegration [raspad] of organic matter: reduction [reduktsiya] by Thienemann, destruction [destruktsiya] by Winberg, decomposition [dekompozitsiya] by Waksman and Lindeman, and so on. An essential feature of decomposition after death is the circumstance that purely chemical oxidation of organic matter apparently does not occur in water, and all "decomposition" processes take place by participation of microorganisms (Kuznetsov, 1939). Of course bacterial processes of destruction [razrushenie] of organic matter in a body of water have an importance that extends far beyond the limits of the problem of productivity (Krys et al., 1935; Waksman and Carey, 1935; Waksman and Renn, 1936; and others).

17. Earlier, we showed that nature, unfortunately, does not permit us to make use of a concept of trophic levels that include forms which are very diverse in their relation to the processes of transformation of energy. Hence, understanding the paths of energy transformation in each particular body of water, from the original organic matter to the object that interests us, becomes the second stage of any actual study of production processes.

The paths of such transformations or, as they are often called, "diagrams of food interrelationships," have repeatedly been made an object of study for selected species in the population. However, as a rule authors restrict themselves only to determining what food groups serve as foods for objects that interest them, most often fish, and refrain from further study of the nutrition of these food organisms, and so on.

In these same works, if a food-chain diagram does include all the organisms in a "vertical section," the organisms are as a rule combined, as Petersen has done, into groups that are as varied and nonuniform as are the trophic-level groups.

The impression exists that such diagrams cannot be anything but extremely complex. Actually, if for example we look at the scheme of Hardy (1925), who unlike other investigators has extended his diagram down to the plankton algae, then the first thing that strikes our eye is the complex flight of arrows representing [page 111] the various food relationships. This latter impression is the more discouraging because it represents the feeding of only one narrow group — the herring.

However, this complexity is somewhat artificial and stems basically from the tendency of investigators to include in their diagram all the groups of organisms encountered in the alimentary tracts of the objects studied, as far as possible. Shorygin has taken a significant step forward in the matter of quantitatively evaluating the importance of food relationships for fishes (unpublished data). He has shown that in the food of 19 species of benthophagous animals of the north Caspian Sea, 138 more or less uniform groups of prey organisms play a part, i.e. there exists the same complexity as other authors have found. However, dividing the prey organisms into important ones (those that make up [25%–75%] of the ration [of the species being studied]), medium ones (those within the range of 5%–25%), and unimportant ones (comprising less than 5%), Shorygin found that only 21 groups belonged in the first division; that is, on the average there was a little more than one dominant prey group per species. If we consider a single species, for example the vobla [*Leuciscus rutilus caspicus*], it appears that one group of prey organisms is in the "important" category (one species — *Dreissena polymorpha*), three groups are "medium," and eleven groups are "weak" — comprising less than 5% of the ration. This important circumstance permits us to hope that diagrams of food interrelationships, worked out with an exact quantitative evaluation of their separate components, may make considerable simplification of the picture possible in each individual case, without introducing appreciable error into the total computation.

To the above we may also add the following. As a rule, such diagrams are constructed for a long interval of time, commonly even for a whole year's cycle. However, seasonal changes in food are a well-known fact. For example, the investigations of Lindeman (1941) clearly indicated changes in food relationships when the analysis was made from the seasonal point of view. Thus, diagrams of the paths of transformation of energy, simplified by the omission of second-grade components and pertaining to a comparatively limited period of time, for which period they will reflect reality quite well, appear to be a very practical means for the quantitative evaluation of the energy processes taking place. In attempting a specific terminology, it seems to me that a useful way to construct a picture of trophic relationships will be to use the methods introduced by Ermakov (1936) for the classification of biocoenological structure. In that event, although the "series" [ryady] of Ermakov do remind us somewhat of the "levels" [urovni] of Hutchinson, they obviously constitute the necessary framework for concrete calculations of energy transformation.[6]

18. Any actual attempt at constructing trophic diagrams will inevitably encounter a series of complicating factors. The first of these will be, unquestionably, the extremely limited data, even of a simple qualitative character, concerning the food of many important water dwellers. In spite of the tremendous literature concerned with the food of fishes—Shorygin (1939) cites more than a thousand titles — the food of invertebrates has almost completely

---

[6] [Ivlev does not appear to use the term *ryad* at all in the text that follows, but he refers often to *zvena*, literally "links" (in a food chain). I have usually translated *zveno* as "step" (of a food pyramid), because this metaphor suggests the reduction in mass that occurs in proceeding from one stage to the next.]

---

escaped the attention
for example, the trop
Sea of Azov, are rarit
is quite unavoidable —
then the whole probler

Even more difficu
in which the transfor
There can be no doul
in the list of question
with great persistence
1941), and it is also ob

Lindeman propose
consumers of energy.
transformation among
much in common, and
it would seem that n
set them apart in a qu

Microorganisms, l
from two points of viev
organisms. A distinctiv
that bacteria, fungi, a
individuals which have
animals and plants. El
groups of an ecosysten
of prey, and that car
food habits. In this se
as the chemical compo
matter dissolved in the
1926; Krogh and Lang

The utilization of
features. Along with
as energy-providing m
serve as suppliers of vi
to death of the orgar
clearly exhibited in th
possibility of the exist
skaya, 1936), but it is
ones (Clarke and Gellis

It may be assume
problem of detritus in
of organic compounds
of these microorganism
in every case to cultur
using as the sole energ

escaped the attention of investigators. Even such schematic constructions as, for example, the trophic step *benthos→plankton*, given by Vorobev for the Sea of Azov, are rarities (cited from Okul, 1941). If in addition — and this is quite unavoidable — we must of necessity work with quantitative estimates, then the whole problem is left dangling in the air.

Even more difficult to study quantitatively are those steps in the process in which the transformers of energy are bacteria and other microorganisms. There can be no doubt about the need to include microbiological processes in the list of questions to be studied. [page 112] This has been emphasized with great persistence by many investigators (see for example, Waksman, 1941), and it is also obvious from all the considerations mentioned earlier.

Lindeman proposes to separate heterotrophic microorganisms from animal consumers of energy. However, as will be shown below, the indices of energy transformation among heterotrophic microorganisms and among animals have much in common, and considering all the aspects of microbiological processes, it would seem that none of them have any special significance that would set them apart in a qualitatively distinct category.

Microorganisms, like other elements of an ecosystem, can be considered from two points of view: as consumers of energy and as food material for other organisms. A distinctive feature of the former process will be the circumstance that bacteria, fungi, and other saprophytic forms utilize the energy either of individuals which have died naturally, or of the products of the metabolism of animals and plants. Elton (1927) has shown that as we proceed into the higher groups of an ecosystem universality increases, in the sense of choice of objects of prey, and that carnivores are the least specialized animals in respect to food habits. In this sense microorganisms are even more universal, inasmuch as the chemical composition of organisms (Ivlev, 1939), and even of the organic matter dissolved in the water, is in the highest degree uniform (Birge and Juday, 1926; Krogh and Lange, 1931).

The utilization of microorganisms as food material also has some special features. Along with the simple utilization of the bodies of microorganisms as energy-providing material, for a number of invertebrate animals bacteria serve as suppliers of vitamins, and their exclusion from a diet invariably leads to death of the organisms being fed. This latter circumstance is especially clearly exhibited in the case of insects, among which there is in general no possibility of the existence of sterile individuals (see the summary by Petrovskaya, 1936), but it is known also for other water animals, including marine ones (Clarke and Gellis, 1935).

It may be assumed that the so-called "detritus feeding," and the whole problem of detritus in general, amounts to the splitting up by microorganisms of organic compounds not assimilated by other forms, and the utilization of these microorganisms as food material. In our experiments it proved possible in every case to culture Chironomidae for several parthenogenetic generations, using as the sole energy-supplying material pure cellulose (filter paper), with

---

cts studied, as
in the matter
hips for fishes
cies of bentho-
niform groups
exity as other
mportant ones
eing studied]),
portant ones
ups belonged
nore than one
, for example
of prey orga-
polymorpha),
— comprising
s us to hope
quantitative
implification
appreciable

ch diagrams
whole year's
For example,
od relation-
view. Thus,
he omission
nited period
ear, to be a
y processes
hat a useful
he methods
gical struc-
remind us
constitute
formation.[6]
inevitably
e, unques-
character,
e tremen-
cites more
ompletely

ut he refers
s "step" (of
proceeding

an intermediate link consisting of an appropriate culture of bacteria which decomposed the latter (Ivlev and Gorbunov, 1944).

19. The concept of "trophic levels" presupposes almost complete consumption of the organisms found on the previous level, by the organisms on the following one.[7] Dissipation of energy by natural death, and in general by its leaving the cycle, is considered (except for respiratory processes) to be negligibly small. However, taking as the quantitative expression of the productive process the formation of some quite definite material, it is easy to demonstrate in any body of water the presence of trophic side-channels which do not lead to the selected "product." In other words, in the interaction of two populations, where one is a food material for the other, the degree of utilization of the former need not by any means reach 100%; on the contrary, as a rule it is utilized only partially, while part of the energy it contains is dispersed into other trophic channels. [page 113] It is necessary to take account of this situation even in the case where these other channels lead to objects that are of interest to us — that is, to the product; for depending on the nature of the steps in the energy transformations, the final result, even though qualitatively identical, will be quantitatively a function of the path it has taken.

For a quantitative evaluation of the production processes it is of only secondary importance to determine the subsequent fate of that part of the energy which escapes outside the limits of the scheme of trophic interactions involving the selected product. The essential element is solely to determine the degree of energy utilization in the consumption (or more generally the utilization — to include the case of saprophytic microorganisms) of one population by another. In other words the question boils down to a simple ecological evaluation of the efficiency of the foraging that takes place under the given environmental conditions.

As a quantitative expression of this phenomenon I have proposed (Ivlev, 1939zh) the *ecotrophic coefficient* [ekotroficheskii koeffitsient]: the ratio of the

---

[7] [The general exposition of the trophic level concept by Hutchinson does not include such a restriction; in fact trophic levels, in principle at least, are meant to be equivalent to Ivlev's "groups of organisms uniform in respect to trophic relationships." However, the above restriction, as well as the other aspects of the trophic level concept that Ivlev criticizes, do appear in the numerical examples of Lindeman (1942). The latter paper was the final published work of a well-loved young ecologist, and is notable for its originality and charm. Nevertheless, it has some serious deficiencies which have confused Ivlev and others, and which have not been given too much attention (Smith, MS, 1955; Slobodkin, 1962). One trouble is that the numerical examples are based on very crude assumptions regarding rate of respiration, rate of "turnover," etc., and the figures used must in some cases be more than doubled to accord with more recent information. More serious is the fact that the energy budgets do not balance. Quoting Smith: "A puzzling feature of Lindeman's analysis is the addition of predation and decomposition to the productivity estimate obtained from standing crops. In the latter estimate, while the standing crop is assumed to replace itself every so often, no account is offered of the fate of the replaced population. It remains, actually, as a net yield in his system. An annual net yield that is 70% of the primary productivity is not imaginable, especially in a lake [Cedar Bog Lake] from which very little is removed. Geologically, the lake would have filled up in a moment." Similar considerations apply to the other examples, Lake Mendota and the Caspian Sea, though these do have an appreciable yield of fish and other products.

It can be urged, of course, that Ivlev's proposals represent a counsel of perfection for which aquatic ecology is not ready even yet, and that for the time being we must still make comparisons between the gross categories plankton, benthos, etc.]

---

size of the daily rat
ration) to the mean
predator's foraging
in terms of strictly d
form of expression, g

where ϵ_i is the unkn
r_i is the daily ration
is the daily increme
be divided by the e
(including its increm
energy base for the
necessary to rememb
for each element of th
great importance in
coefficient is a measu
step, without taking
predator's body.

20. The interre
has been the them
majority of quantit
value for solving th
Lotka (1925) and Vol
of collisions, a purely
gases. According to
prey is proportional
of hunting in a stab
concentration of prey
exists over a long p
1941), neverthelešs,
tively short time in

---

[8] [The ecotrophic co
interval (of the order of 1
Ivlev later (Section 25) is
nition, which may be des
consumption to its prey'
this is:

where *t* will in general be

e of bacteria which

most complete con-
by the organisms
ath, and in general
atory processes) to
expression of the
terial, it is easy to
ide-channels which
the interaction of
her, the degree of
%; on the contrary,
ergy it contains is
ry to take account
els lead to objects
ding on the nature
even though qua-
ath it has taken.
esses it is of only
that part of the
ophic interactions
lely to determine
ore generally the
ms) of one popu-
simple ecological
under the given

proposed (Ivlev,
the ratio of the

oes not include such
quivalent to Ivlev's
he above restriction,
s, do appear in the
shed work of a well-
theless, it has some
een given too much
erical examples are
urnover," etc., and
recent information.
Smith: "A puzzling
to the productivity
ing crop is assumed
aced population. It
0% of the primary
which very little is
onsiderations apply
ave an appreciable

erfection for which
make comparisons

---

size of the daily ration (more exactly, of a particular element in the daily ration) to the mean density of the same element within the bounds of the predator's foraging area. However, since it is not always possible to work in terms of strictly daily quantities, it is more convenient to use a more general form of expression, given by the equation:

$$\epsilon_i = \frac{\sum^{t} r_i}{{}_0B_i + \sum^{t-1} \Delta B_i}$$

where ϵ_i is the unknown ecotrophic coefficient for a time t (in 24-hr days), r_i is the daily ration, ${}_0B_i$ is the original biomass of the given food and ΔB_i is the daily increment of the food. From this, if the quantity of food used be divided by the ecotrophic coefficient, we obtain a figure for the biomass (including its increment during the given interval of time) that served as the energy base for the performance of the observed energy transfer.[8] It is only necessary to remember that a determination of the size of ϵ_i must be made for each element of the ration separately, insofar as such element is of sufficiently great importance in the food of the species in question. Thus, the ecotrophic coefficient is a measure of the intensity of utilization of food material at each step, without taking account of the further transformation of energy in the predator's body.

20. The interrelationships of populations in the system predator → prey has been the theme of numerous ecological investigations. However, the majority of quantitative generalizations on the question are of very little value for solving the problem before us. In their theoretical constructions Lotka (1925) and Volterra (1933, 1937) start out from the principle of frequency of collisions, a purely physical concept taken from the theory of the kinetics of gases. According to this principle the degree of interaction of predators and prey is proportional to the product of their abundances, whence the success of hunting in a stable population of predators must be proportional to the concentration of prey. Even if such proportionality be possible in a system that exists over a long period of time and includes many generations (Severtsov, 1941), nevertheless, to evaluate intensity of consumption during a comparatively short time interval it is necessary to start from different postulates.

---

[8] [The ecotrophic coefficient defined as above, where t will typically be a rather short time interval (of the order of 1 or a few days), may be called the "static" ecotrophic coefficient. When Ivlev later (Section 25) is treating the process of production as a whole, he uses a different definition, which may be designated the "dynamic" ecotrophic coefficient: the ratio of a predator's consumption to its prey's *production*, rather than standing crop. In the symbols used above, this is:

$$\frac{\sum^{t} r_i}{\sum^{t} \Delta B_i}$$

where t will in general be a rather long time interval, typically a year.]

Apart from that, in a series of experimental verifications of the theses of Lotka and Volterra, Gause (1934, 1934a, 1934b, 1935) and Smaragdova (1936) have shown that these authors' hypotheses are realized only under infrequent, specially-created circumstances.

[page 114] I have proposed a different starting point for analyzing this question (Ivlev, 1943a), which is the proposition that the intensity of feeding [food intake] by an animal would be proportional to the difference between the maximal and the actual ration. From this it follows that the size of a single ration [that taken during one feeding period] must be given by the equation:

$$r = R\,(1 - e^{-kp})$$

where R and r correspond to the maximal and the actual rations, p is the abundance of food, and k is a coefficient peculiar to each system.

Experimental verification of these theoretical ideas gave satisfactory results, in the course of which the necessity for analyzing certain related conditions became evident. One of these factors was the fact that intensity of feeding increased when the prey was distributed in aggregates. Analysis of this effect led to the formulation of a general principle of aggregative influence, in which the food intake now corresponds to the expression:

$$r = R[1 - e^{-\chi p + \chi \zeta}]$$

in which ζ and χ represent, respectively, an index of aggregation (degree of nonuniformity of distribution) and the corresponding proportionality coefficient.

21. It is evident that the techniques of modern hydrobiological investigations, suitably modified, do make it possible to estimate the ecotrophic coefficient in each individual case. However, such a solution of the problem, by reason of its very great magnitude and difficulty, would bring to naught every attempt at a quantitative analysis of the productive process. Consequently, the discovery of general laws and patterns that characterize the phenomenon must be one of our basic tasks in solving the productivity problem. My own efforts along these lines should not be overrated, because in the first place, they deal with the question of the *rate* of feeding and not with daily rations — which obviously are not the same things; and secondly, a whole group of additional accessory factors was disregarded. Moreover, an example abstracted from natural conditions represents a special case because of the complete absence of such factors as interspecific competition, while the problem of selective feeding was virtually eliminated inasmuch as all of the benthos was eaten up at the end of the experiment. Yet from information already at hand, it must be supposed that such factors can play a very important role in the ecological interaction of predator and prey populations, and will affect both the direction and the final result of the process (Shorygin, 1939,

---

1940; Ivlev, 1943b, 194
Besides that, the energy
at different prey densiti
results, in some cases red
(Ivlev, 1943a).

This "ecological" pa
presents greatest difficult
that will simplify quanti

22. The last basic
the question of the ene
by the animals involve
is concerned specifically
to show that there is a
problem.

[page 115] There ar
paths of energy transfo
each other generally but
Tauson, 1933, 1935; Terr
scheme is especially sim
following:

Q : the quantity of

Q' : the energy used

Q_R: the energy in t

Q_t : the energy of p
teploty]

Q_e : the energy of ext

Q_w: the energy of int

Then the whole energy b
the equation:

Q

Notice that Q_t, the prim
are accompanied by an i
heat, but it is not the s
fact is rather important, si

---

[9][Or possibly: "but not its
eduyushchim prevrashcheniem v

eses of Lotka
gdova (1936)
r infrequent,

nalyzing this
ty of feeding
nce between
ze of a single
he equation:

ns, *p* is the

satisfactory
related con-
intensity of
Analysis of
ve influence,

ion (degree
nality coeffi-

gical inves-
ecotrophic
he problem,
to naught
ess. Conse-
the pheno-
y problem.
use in the
d not with
secondly, a
oreover, an
se because
tion, while
uch as all
nformation
important
s, and will
ygin, 1939,

1940; Ivlev, 1943b, 1943v; Larsen, 1936; Zheltenkova, 1939; and others). Besides that, the energy expenditure by predators during their hunting time, at different prey densities, can also lead to completely different quantitative results, in some cases reducing to zero the net return from the situation involved (Ivlev, 1943a).

This "ecological" part of the problem of aquatic production is the one that presents greatest difficulty for experimental attack and for discovering patterns that will simplify quantitative evaluation of productive processes.

22. The last basic division of the problem has a more favourable aspect: the question of the energy transformations of the organic matter ingested by the animals involved. Actually Lindeman's "correction for respiration" is concerned specifically with the analysis of this factor. However, I will try to show that there is a more rational and correct way of approaching the problem.

[page 115] There are in existence a number of schemes describing the paths of energy transformation within a living organism, which resemble each other generally but differ in detail (Rubner, 1902, 1908; Armsby, 1917; Tauson, 1933, 1935; Terroine and Wurmser, 1922). The last-mentioned authors' scheme is especially simple and suitable for futher discussion. Consider the following:

Q : the quantity of energy that an organism gets in its food

Q' : the energy used for growth

Q_R : the energy in the unutilized part of the food (the part eliminated)

Q_t : the energy of primary heat [energiya pervichno obrazuyushcheĭsya teploty]

Q_v : the energy of external work [energiya vneshneĭ raboty]

Q_w : the energy of internal work [energiya vnutrenneĭ raboty]

Then the whole energy balance of a growing organism will be expressed by the equation:

$$Q = Q' + Q_R + Q_t + Q_v + Q_w$$

Notice that Q_t, the primary heat, is the result of exothermic reactions that are accompanied by an inevitable loss of part of the energy in the form of heat, but it is not the subsequent transformation of work into heat.[9] This fact is rather important, since it is known that heat, once formed, can no longer

---

[9] [Or possibly: "but not its subsequent transformation into the heat of work" — no ne posleduyushchim prevrashcheniem v teplo raboty.]

be utilized by an organism (Oppenheimer, 1921), and for poikilothermic water organisms it is lost without being of any benefit.[10]

---

[10] [Other investigators have not been able to identify this "primary heat" (Q_t). The following passage, translated from Winberg (1956, p. 201–203), suggests some reasons for the apparent surplus of energy which Ivlev discovered in his 1939 experiments, and which was at least partly responsible for his including primary heat in the equation of the above paragraph.

"Ivlev postulates that, in addition to the energy incorporated into the body structure and that used for external and internal work, the physiologically useful energy ($Q - Q_R$) also includes a "primary heat production" which cannot be utilized by poikilothermal organisms. I will not dwell here on the meaning of "primary heat," but will try to show how Ivlev links his concepts with experimental data. He determined the total amount of food energy absorbed by a carp during the growing season by the nitrogen-balance method. In the particular case it was equal to 1829 cal. The energy of the gain in weight was found by weighing and from determinations of the calorific content of the body of the fish (573 kcal). The energy value of the excreta was computed from the weight and calorific value of the faeces and from the amount of nitrogen in the urine, assuming that the urinary nitrogen was in the form of urea (454 kcal). The "internal work" was determined from respiration and the "oxycalorific coefficient" (150 kcal). To estimate the "external work" it was assumed that the amount of energy expended by the carp in movement was 20% of the "internal work" (30 kcal). Thus, all the quantities were found that make up the total amount of absorbed energy, according to Ivlev's concepts, with the exception of the "primary heat." This last quantity was found by difference:

$$Q - (Q' + Q_R + Q_w + Q_v) = Q_t$$

and it turned out to be very considerable — 622 kcal, which is 45% of the physiologically useful energy.

There is a fundamental objection to estimating "primary heat" from this difference. The entire energy which corresponds to the amount of oxygen consumed was taken into consideration when computing the "external and internal work." The applicability of the first law of thermodynamics to living organisms was firmly established by the classical experiments on energy balance in physiology. Since this is so, then for aerobic metabolism there is not and cannot be any other source of energy than what is released in the oxidation of food. Therefore — as is well known — the physiologically useful energy must be fully accounted for by the sum of the energy of weight increase and the energy represented by respiration. In ideally precise experiments on energy balance the difference that Ivlev accepts as the magnitude of the "primary heat" must be equal to zero.

The question then arises, where does the difference come from that Ivlev identifies as "primary heat" in balancing the energy budget for carp? When the observations on nitrogen balance were being made, respiration was not measured. The necessary values were taken from a previous work by Ivlev (1938), concerning which we noticed earlier (page 100) that in measuring the metabolic rate of carp Ivlev had obtained unusually low values because the measurements were made in winter using greatly exhausted specimens. These particular data were accepted for computing the magnitude of the "internal work," and as a result the latter has a very low value. From table 1 of Ivlev's paper, the average weight of a carp was equal to 180 g during the growing season. In this event the expected rate of consumption of oxygen at 18.5 C (the average temperature of the growing season) is 19.1 ml O_2/hr, by equation (5.4.1). If the growing period lasts 2760 hr the oxygen consumption of one fish during the entire season is 52.7 litres; this corresponds to 260 kcal. There is no doubt that even this is much too low an estimate, if only because metabolic rate does not increase linearly with temperature, and therefore the contribution of the periods of above-average temperature will be greater, relatively, than what is indicated by a computation made from the "average" temperature. Furthermore, there is no question that the metabolism of carp moving and feeding in a pond is considerably higher than the rate of oxygen consumption of unfed fish in a respirometer. In view of these considerations, the true values of Q_w and Q_v must be much larger than those in Ivlev's paper, and the difference:

$$Q - (Q' + Q_R + Q_w + Q_v) = Q_t$$

must be correspondingly smaller. Furthermore, we must not forget that the total amount of food consumed (Q) was computed from nitrogen metabolism, on the basis of an estimate of the contents of the digestive tract and analyses of food organisms, i.e. a large number of assumptions and approximations were necessary. The final result of these calculations could easily differ from the true food consumption by an amount large enough to explain the remainder of the difference under discussion, which as N. V. Puchkov (1954) aptly observes, represents 'unaccounted expenditures.' "

Obviously, if the concept "primary heat" is not applicable to aquatic poikilotherms, Ivlev's "energy coefficient of growth of the 3rd order" becomes meaningless, and as far as I know no one has tried to put it to any practical use.]

On the basis of th
of energy transformation
ductivities of Terroine a
energy utilization coeffic
(1939, 1939a). The disti
those proposed by the
statistics of Terroine and
microbiology and are not
The following statist

K_1 (energy coeffici

K_2 " "

K_3 " "

It is evident that all
else: in the first case, to
second, to the assimilated
to the gross energy less a
organism *in statu quo.*

Obviously, the first
analysis of the productio
trophic coefficient, or foo
of productivity," of the
to a whole trophic level.[11]

23. Let us consider
coefficients of growth.

The most interesting
initial stages of animal gr
1909; Pfül, 1925; Terroine
among all vertebrates, from
growth an increment of 1
animal to be excluded is
to 29,000 cal. Ivlev (1937,
has determined the growt
vertebrates: Protista, worm
Rubner's law was complete

---

[11] [This is true only if *all* of
ganisms of level *n* — a situation t
concept.]

[12] [Rubner's law is that "th
the same per kilogram in all speci

ikilothermic water

heat" (Q_t). The fol-
easons for the apparent
ch was at least partly
agraph.
o the body structure
energy ($Q - Q_R$) also
ilothermal organisms.
show how Ivlev links
food energy absorbed
the particular case it
ing and from determi-
y value of the excreta
e amount of nitrogen
4 kcal). The "internal
150 kcal). To estimate
the carp in movement
found that make up
the exception of the

physiologically useful

this difference. The
en into consideration
first law of thermo-
nts on energy balance
cannot be any other
is well known — the
the energy of weight
periments on energy
heat" must be equal

t Ivlev identifies as
rvations on nitrogen
ues were taken from
0) that in measuring
se the measurements
data were accepted
atter has a very low
qual to 180 g during
ygen at 18.5 C (the
.4.1). If the growing
season is 52.7 litres;
low an estimate, if
d therefore the con-
tively, than what is
ermore, there is no
derably higher than
these considerations,
, and the difference:

otal amount of food
estimate of the con-
ber of assumptions
could easily differ
e remainder of the
s, represents 'unac-

oikilotherms, Ivlev's
s far as I know no

On the basis of the equation above the following quantitative indices of energy transformation have been proposed: the gross and true energy productivities of Terroine and Wurmser; the energy effect of Tauson; and the energy utilization coefficients of the first, second, and third orders of Ivlev (1939, 1939a). The distinctive feature of my coefficients, as compared with those proposed by the other authors cited, stems from the fact that the statistics of Terroine and Wurmser, and also of Tauson, are specially suited to microbiology and are not very convenient when applied to animal material.

The following statistics are most universal:

$$K_1 \text{ (energy coefficient of growth of the 1st order)} = \frac{Q'}{Q}$$

$$K_2 \text{ " " " " " " 2nd "} = \frac{Q'}{Q - Q_R}$$

$$K_3 \text{ " " " " " " 3rd "} = \frac{Q'}{Q' + Q_t}$$

It is evident that all these coefficients are ratios of growth to something else: in the first case, to the gross energy in the food (energy brutto); in the second, to the assimilated energy of the food (energy netto); and in the third, to the gross energy less all losses that occur in the course of maintaining the organism *in statu quo*.

Obviously, the first of these statistics is of special importance for the analysis of the production process, for it is the reciprocal of the so-called trophic coefficient, or food coefficient. Notice that Hutchinson's "efficiency of productivity," of the type λ_n/λ_{n-1}, is essentially the same index, applied to a whole trophic level.[11]

23. Let us consider some of the characteristic features of the energy coefficients of growth.

The most interesting of their properties is their uniformity during the initial stages of animal growth. A number of authors (Tangl, 1918; Fridental, 1909; Pfül, 1925; Terroine and Wurmser; Ivlev; Scholz, 1933) have shown that among all vertebrates, from fishes to anthropoid apes, during the early stages of growth an increment of 1 g of living substance requires 4000 cal. The only animal to be excluded is man, [page 116] for whom this quantity increases to 29,000 cal. Ivlev (1937, 1937a, 1937b, 1939a, 1939 of the Latin references) has determined the growth coefficients for a number of species of water invertebrates: Protista, worms, molluscs, and arthropods, in the course of which Rubner's law was completely confirmed.[12] Finally, Terroine and Wurmser, Tau-

---

[11] [This is true only if *all* of the production (growth) at level n–1 is consumed by the organisms of level n — a situation that Ivlev regarded as part of the definition of the trophic level concept.]

[12] [Rubner's law is that "the amount of energy required for doubling the birth weight is the same per kilogram in all species except man" (Brody, 1945, p. 47).]

son, Tamija (1932), and other microbiologists have obtained the same figure for heterotrophic microorganisms — bacteria and yeasts. Thus, the constancy of the initial size of the energy coefficients of growth must be considered as firmly established. To this may be added the similarity between the above examples and the processes of energy utilization during embryonic life (Needham, 1931) and during post-embryonic development (Ivlev, 1939).

No less remarkable is the independence of external conditions exhibited by the energy coefficients: even a change of temperature within broad limits is not capable of affecting their absolute magnitude (Terroine and Wurmser; Rubner; Needham; Bily, 1938). On the other hand their absolute size does depend on the chemical composition of the food. Terroine et al. (1927), Tauson (1935a) and Ivlev (1939b) have shown that substances of high calorific content give lower growth coefficients than do those of lower calorific content such as carbohydrates. However, this fact need not have any special importance for the production problem, in view of the above mentioned constancy of the chemical composition of living organisms.

Some change in a growth coefficient can occur as a result of the physiological state of the organism. For example, prior starvation leads to better utilization of energy (Matsui and Oshima, 1935; Ivlev, 1939d).

However, for our problem greatest interest attaches to the changes that these coefficients undergo with age. Starting from an original magnitude approximately equal to 0.35, the energy coefficients begin to decrease as the organism grows, and they become zero at the moment of completion of growth. This decrease is quite regular, resembling a quadratic parabola as a first approximation (Ivlev). However, a more exact representation of the decrease of the growth coefficients with age will apparently be one of the reciprocal curves of the catenary [odna iz retsiproknykh krivykh tsepnoi linii] (Janisch, 1927).

The above circumstance was not taken into consideration by Lindeman in his computation of "corrections for respiration." He noted the lack of agreement between my data and the values obtained by Moore (1941), but this can be explained by the fact that we worked with different age-groups of fish.

If we accept a parabola as a sufficiently close representation of the change in the energy coefficients of growth with age, then there is a possibility of calculating values of these coefficients for each age-group of any animal from observed parameters — the original size of the coefficient, and the time that growth ceases (which is easily ascertainable). In this way the relation between the quantity of energy consumed during the whole period of growth and the quantity of energy that is utilized for growth may be determined (Ivlev, 1939a). In other words, there is a chance of estimating one of the basic quantitative parameters of the production process without resorting to tedious experiments.

24. Numerous facts indicate the necessity for careful analysis of all the steps in the series of energy transformations if the actual course of any production process is to be ascertained. The farther away the group of organisms

---

chosen as a measu
matter, the more
the process.
The bulk of
qualitative connec
put in and the fi
in fish culture (see
tive relation betw
system.
Winberg (193
relation between
matter synthesiz
demonstrate the i
Demoll and a
relationship be de
and that of the fi
Finally, the
comparison of ben
quantitative rela
of solving the pro
In his compu
matter) from one
loss of 90% of th
0.1 of the prima
three, 0.001, and
arbitrary.
Juday (1940
observed quantiti
analyzing the re
facto, it seems t
concept of trop
of] both an ext
to another and,
great a utilizatio
Besides this,
process used by
after introducing
be completely c
"efficiency of pr
to unity.
In the work
According to Li
significant coeffi
of water. It sho

ained the same figure for
hus, the constancy of the
be considered as firmly
een the above examples
bryonic life (Needham,
, 1939).
nal conditions exhibited
ure within broad limits
Terroine and Wurmser;
their absolute size does
ine et al. (1927), Tauson
of high calorific content
r calorific content such
y special importance for
ioned constancy of the

a result of the physiolo-
rvation leads to better
1939d).
hes to the changes that
an original magnitude
egin to decrease as the
of completion of growth.
arabola as a first approx-
ion of the decrease of
of the reciprocal curves
i ĭinii] (Janisch, 1927).
ideration by Lindeman
noted the lack of agree-
Moore (1941), but this
different age-groups of

sentation of the change
e is a possibility of cal-
up of any animal from
ent, and the time that
ay the relation between
riod of growth and the
be determined (Ivlev,
one of the basic quanti-
esorting to tedious ex-

careful analysis of all
e actual course of any
the group of organisms

---

chosen as a measure [page 117] of production stands from the primary organic matter, the more difficult it becomes to predict the quantitative result of the process.

The bulk of the data concerning pond fertilization demonstrate only a qualitative connection (and this by no means all the time) between the fertilizer put in and the fish produced, as is shown by the conclusions of specialists in fish culture (see Demoll's review). There can be no question of any quantitative relation between these two steps, which are at opposite ends of the ecosystem.

Winberg (1937) and Ivlev (1938) have both made an attempt to find a relation between the fish production in ponds and the quantity of organic matter synthesized during the same period. The results obtained merely demonstrate the impossibility of using such comparisons.

Demoll and also Kreutner (1934) have shown that neither can any definite relationship be demonstrated between the degree of development of plankton and that of the fish stock.

Finally, the very varied values of F/B (Alm's (1922) coefficient which is a comparison of benthos and fish production), also testify to the complexity of the quantitative relationships in production processes, and the impossibility of solving the problem by dividing one quantity by another.

In his computations Petersen assumes that the transfer of energy (or organic matter) from one uniform group of organisms to another takes place with the loss of 90% of the matter at each step. Thus, in a system containing one step, 0.1 of the primary organic matter is transferred; with two steps, 0.01; with three, 0.001, and so on. The coefficient chosen — 10 — was of course completely arbitrary.

Juday (1940), Bruevich (1939, 1941), and Lindeman (1941) present the observed quantities of organic matter found at different trophic levels. Without analyzing the reliability of the quantities obtained, and accepting them *de facto*, it seems to me that they merely demonstrate the inadequacy of the concept of trophic levels. Supporting this conclusion, there are [examples of] both an extremely small percentage transfer of energy from one level to another and, what is especially revealing, also the opposite situation — too great a utilization of the energy of the previous level.

Besides this, from the method of calculating the course of the productive process used by Lindeman it would seem to follow as a matter of course that, after introducing all the corrections, the remaining "adjusted" energy should be completely carried over into the next trophic level. Hence Hutchinson's "efficiency of productivity" for two adjacent levels should in all cases be equal to unity.

In the works cited there are figures for the utilization of solar radiation. According to Lindeman this is 0.1%, according to Juday 0.4%. This is a very significant coefficient, suggesting a high utilization of solar energy by a body of water. It should be remembered that comparable coefficients for the most productive agricultural practices, for the vegetative period only, give values of the order of 2–3% (Doyarenko, 1925).

25. The statistics I have proposed, the ecotrophic coefficient (ϵ) and the energy coefficient of growth (K), are true reflections of energy transformations that take place in a body of water. These coefficients, estimated by some appropriate method for each step [in a food pyramid], make it very easy to assess [opredelit'] any part of the production process. Their application is very simple.

Let the production of some group of organisms (a population) be represented by the quantity W. It is made up [of organic matter obtained] from the utilization of n populations [page 118] of food groups, i.e.:

$$W = W_1 + W_2 + W_3 + \ldots + W_n$$

The productions of the food populations will similarly be expressed by the quantities:

$$v_1, v_2, v_3 \ldots v_n$$

Consequently, the whole course of the production process at a given step can be expressed in this manner.[13]

$$W_1 = v_1K_1\epsilon_1; \quad W_2 = v_2K_2\epsilon_2; \quad W_3 = v_3K_3\epsilon_3; \quad W_n = v_nK_n\epsilon_n$$

from which:

$$W = v_1K_1\epsilon_1 + v_2K_2\epsilon_2 + v_3K_3\epsilon_3 + \ldots. + v_nK_n\epsilon_n$$

Inasmuch as the value of K is determined by characteristics (principally the age) of the feeding organism, then for any given step:

$$K_1 = K_2 = K_3 = \ldots. = K_n$$

Hence, it is possible to represent the sum given above in the general form:

$$W = K\ \Sigma v_i\epsilon_i$$

This equation portrays the relationship between the production of the two elements in one trophic step, and makes it possible to estimate the unknown production of any population of heterotrophic organisms from information on the production of its food populations and the appropriate coefficients.

Obviously, if it is desired to express the whole process of production quantitatively the same operation must be carried out for all previous steps

---

[13] [The expressions shown are those that flow from the argument. In the equations actually given by Ivlev, the W values are made equal to $v/K\epsilon$, presumably because of a slip.]

---

in the trophic cycle. If
arise in using the princip
to introduce any kind c
factors making for incon
ficients used.

We may observe th
trophic relationships, con
extent will correspond t
of energy from the cycle
production will be equal t
matter multiplied[14] by th

Considering the tre
the quantitative analysis
obtaining numerical valu
sary elements, we must
as is the biological produ
methods. Furthermore,
nature is completely unde
tions involved have been

[Russian and foreign work
been translated. Ivlev's name app
1939," and the foreign reference
in footnotes or foreword have bee

AN SSSR = *Akademi*
AN UkrSSR = *Akademiy*
VNIRO = *Vsesoyuz*

Aleev, B. 1934. Mikrobiol.,
1936. Biokhimiya, 1: 1

Atstsi, Dzh. 1932. [Agricult

Bily, M. 1938. Tr. gidrobiol

Borutsky, E. 1939. Tr. lim
1939a. The same, 196.

Brilliant, V. A. 1943. Pri

Brotskaya, B., and L. Zenke
1939. Tr. VNIRO, 4.

Bruevich, S. 1936. Sb. "Ak
1939. Doklady AN SS
[*page 119*]
1941. Tr. po kompleks.

Winberg, G. 1934. Tr. limn
1936. Zoolog. zhurn., 1
1937. Tr. limnol. st. v

---

[14] [The original says "divid

in the trophic cycle. If this be done, the manifold errors that unavoidably arise in using the principle of trophic levels will vanish, for there is no need to introduce any kind of supplementary adjustments, inasmuch as all the factors making for incomplete utilization of energy are included in the coefficients used.

We may observe that in the case of the simplest imaginable scheme of trophic relationships, consisting of a consecutive series of steps (which to some extent will correspond to the trophic levels, provided the possibility of loss of energy from the cycle at each step is taken into account), the unknown production will be equal to the magnitude of the primary production of organic matter multiplied[14] by the product of all the coefficients.

Considering the tremendous difficulties inherent in problems involving the quantitative analysis of production processes, difficulties associated with obtaining numerical values for the statistics describing any of the four necessary elements, we must recognize that a phenomenon as complex by nature as is the biological production of a body of water cannot be resolved by simple methods. Furthermore, any kind of approximation is admissible only if its nature is completely understood and if the possible ramifications of the assumptions involved have been carefully scrutinized.

REFERENCES

[Russian and foreign works are separated, the former being first; titles of Russian works have been translated. Ivlev's name appears in both lists, but there can be confusion only in the case of "Ivlev, 1939," and the foreign reference of this date has been noted in the text. References cited by the translator in footnotes or foreword have been added.]

AN SSSR = *Akademiya Nauk SSSR*
AN UkrSSR = *Akademiya Nauk Ukrainskoi SSR*
VNIRO = *Vsesoyuznyi N.-I. Institut Morskogo Rybnogo Khozyaistva i Okeanografii*

Aleev, B. 1934. Mikrobiol., **3**: 4.
1936. Biokhimiya, **1**: 1.

Atstsi, Dzh. 1932. [Agricultural ecology.]

Bily, M. 1938. Tr. gidrobiolog. st. AN UkrSSR, **16**.

Borutsky, E. 1939. Tr. limnolog. st. v Kosine, **22**: 156.
1939a. The same, 196.

Brilliant, V. A. 1943. Priroda, **5**.

Brotskaya, B., and L. Zenkevich. 1936. Zoolog. zhurn., **15**: 1.
1939. Tr. VNIRO, 4.

Bruevich, S. 1936. Sb. "Akademiku Vernadskomu."
1939. Doklady AN SSSR, 25.
[*page 119*]
1941. Tr. po kompleks. izuch. Kasp. morya, **14**.

Winberg, G. 1934. Tr. limnolog. st. v Kosine, **18**: 5–24.
1936. Zoolog. zhurn., **15**(4): 587–603.
1937. Tr. limnol. st. v Kosine, **21**: 61–73.

---

[14] [The original says "divided"; see footnote 13.]

1937a. The same, **21**: 75–87.
1939. Nauchno-metod. zap. Gl. upr. po zapovednikam, **4**: 39–51.
1956. [Rate of metabolism and food requirements of fishes.] Nauchnye Trudy Belorusskogo Gos. Universiteta, Minsk. 253 p.

WINBERG, G., AND A. IVANOVNA. 1935. Tr. limnol. st. v Kosine, **20**: 5–34.

WINBERG, G., AND L. YAROVITSINA. 1939. The same, **128**.

WINBERG, G., AND Z. KUZNETSOVA. 1939. The same, **22**: 144.

GAUSE, G. 1934. Zoolog. zhurn., **13**.
1934a. The same.
1934b. Byull. Mosk. o-va ispyt. prirody, Otd. biologii, **43**: 1.
1935. Zool. zhurn., **14**.

GUSEVA, K. 1938. Mikrobiol., **7**: 3.

DOYARENKO, A. 1925. Nauch. selskokhoz. zhurn.

ELEONSKY, A. 1936. [Fish culture in natural and artificial waters.]

ERMAKOV, M. 1936. Tr. gidrobiolog. st. AN UkrSSR.

ZHADIN, V. 1940. Tr. zoolog. inst. AN SSSR, **5**: 3–4.

ZHELTENKOVA, M. 1939. Tr. VNIRO, **10**.

ZENKEVICH, L. 1934. Tr. faun. konf. zool. inst. AN SSSR, 3–8 fevr. 1932 g.

IVLEV, V. 1937. Byull. eksperim. biolog. i med. **3**: 2.
1937a. The same, **3**: 281.
1937b. The same, 284.
1938. Byull. Mosk. o-va ispyt. prir., Otd. biologii, **57**: 4.
1939. Zool. zhurn., **18**: 2.
1939a. Byull. Mosk. o-va ispyt. prir., Otd. biologii, **58**: 1.
1939b. The same, **4**.
1939v. Mikrobiol., **8**: 8.
1939g. Doklady AN SSSR, **25**: 1, 87.
1939d. The same, 90.
1939e. Nauchno-method. zap. Gl. upr. po zapovednikam, **5**.
1939zh. [A quantitative study of the consumption of benthos by fishes.] (MS).
1940. [Effect of number stocked upon the growth of carp.] (MS).
1944. Zool. zhurn., **23**.
1943a. [Density and distribution of food as factors determining the size of the ration.] (MS).
1943b. [An attempt at an experimental analysis of the phenomenon of selectivity for food.] (MS).
1943v. [Concerning the relationship of food selectivity to the character of the distribution of prey organisms.] (MS).
1955. [Experimental ecology of fish feeding.] 252 p. Moscow.

IVLEV, V., AND M. MUKHAREVSKAYA. 1940. Doklady AN SSSR, **27**: 1.

IVLEV, V., AND K. GORBUNOV. 1944. [Bacteria as intermediate links in the nutrition of water animals.] (MS).

KARZINKIN, G. 1936. Zoolog. zhurn., **15**: 2.

KIREEVA, M., AND T. SHCHAPOVA. 1938. Tr. VNIRO, **7**.

KIRSANOV, A. 1930. [Mitscherlich's theory, its analysis and practical applications.]

KOSTYCHEV, S. 1937. [Plant physiology.]

KUZNETSOV, S. 1939. Tr. limnol. st. v Kosine, **22**.

LIPIN, A., AND N. LIPIN. 1935. [Water macrophytes and their relation to the aquatic fauna.] (MS).

LYUBIMENKO, V. 1935. [Photosynthesis and chemosynthesis in the plant world.]

MOROZOVA-VODYANITSKAYA, N. 1936. Tr. Sevastop. biol. st., **5**.

MURAVEISKY, S. 1936. Zoolog

OKUL, A. 1941. Ibid., **20**: 2.

PETROVSKAYA, O. 1936. Uspe

ROSSOLIMO, L. 1934. Tr. limn

SEVERTSOV, S. 1941. [Populat

SKADOVSKY, S. 1937. Zoolog.

SMARAGDOVA, N. 1936. Ibid.,

SMIRNOV, V. 1924. Izv. Gos. g

TAUSON, V. 1933. Mikrobiolog
1935. The same, **4**: 166.
1935a. The same, 317.

FRANTSEV, A. 1932. The same

SHORYGIN, A. 1939. Zoolog. zh
1940. [The food and fo
North Caspian Sea.] (MS).

ALM, G. 1922. Verhandl. inter

ARMSBY, H. P. 1917. The nutr

ATKINS, W. 1926. J. du Cons.,

BIRGE, E., AND CH. JUDAY. 192

BODENHEIMER, F. 1932. Zt. an

BRODY, S. 1945. Bioenergetics

CLARKE, G., AND R. OSTER. 193

CLARKE, G., AND S. GELLIS. 193

CONTAG, E. 1930. Zt. für Fisch

COOPER, L. 1933. J. mar. biol. a

DEMOLL, R. 1925. Teichdüngu

EHRKE, G. 1931. Planta, **13**.

ELTON, Ch. 1927. Animal ecolo

FRIDENTAL, H. 1909. Zt. allg.

GAARDER, T. 1932. Bergens Mu

GAARDER, T., AND H. Gran. 192

GESSNER. 1933. Ber. deutsch. B
[*page* **120**]

GRAN, H. 1927. Rep. norweg. fi
1929. Rapp. proc. verb. R
1930. Scr. utg. av det Nor

GRAN, H., AND BIRGITHE. 1926.
Kl., **6**.

HARDY, A. 1925. Fish. invest., S

HEINRICH, K. 1934. Int. Rev. g

VAN HILLE, J. 1938. Rec. trav.

HUTCHINSON, G. 1942. Recent a

–51.
] Nauchnye Trudy Belorus-
20: 5–34.
r. 1932 g.
by fishes.] (MS).
S).
ng the size of the ration.]
omenon of selectivity for
aracter of the distribution
: 1.
s in the nutrition of water
l applications.]
ion to the aquatic fauna.]
lant world.]

Muraveisky, S. 1936. Zoolog. zhurn., **15**: 4.

Okul, A. 1941. Ibid., **20**: 2.

Petrovskaya, O. 1936. Uspekhi sovr. biologii, **5**: 5.

Rossolimo, L. 1934. Tr. limnol. st. v Kosine, **17**.

Severtsov, S. 1941. [Population dynamics and adaptive evolution of animals.]

Skadovsky, S. 1937. Zoolog. zhurn., **16**: 1.

Smaragdova, N. 1936. Ibid., **15**.

Smirnov, V. 1924. Izv. Gos. gidrolog. inst., **8**.

Tauson, V. 1933. Mikrobiolog., **2**: 1.
1935. The same, **4**: 166.
1935a. The same, 317.

Frantsev, A. 1932. The same, **1**: 2.

Shorygin, A. 1939. Zoolog. zhurn., **18**: 1.
1940. [The food and food-interrelationships of some benthophagous animals of the North Caspian Sea.] (MS).

Alm, G. 1922. Verhandl. internat. ver. limnol., **1**.

Armsby, H. P. 1917. The nutrition of farm animals.

Atkins, W. 1926. J. du Cons., **1**.

Birge, E., and Ch. Juday. 1926. Proc. nat. acad. of sci., **12**.

Bodenheimer, F. 1932. Zt. ang. entomol., **19**.

Brody, S. 1945. Bioenergetics and growth. Reinhold Publ. Corp., New York.

Clarke, G., and R. Oster. 1934. Biolog. bull., **67**.

Clarke, G., and S. Gellis. 1935. Ibid., **68**: 2.

Contag, E. 1930. Zt. für Fisch., **29**.

Cooper, L. 1933. J. mar. biol. assoc., United Kingdom, **18**: 2.

Demoll, R. 1925. Teichdüngung. Handb. Binnenfisch., **4**.

Ehrke, G. 1931. Planta, **13**.

Elton, Ch. 1927. Animal ecology.

Fridental, H. 1909. Zt. allg. Physiol., **9**.

Gaarder, T. 1932. Bergens Museum Arbok. 1932. Nat. Rekke, **3**.

Gaarder, T., and H. Gran. 1927. Cons. perm. inter. expl. de la mer, Rapp. et proc. verb.

Gessner. 1933. Ber. deutsch. Botan. Ser., **51**.
[*page* 120]

Gran, H. 1927. Rep. norweg. fish. and mar. invest., **3**: 8.
1929. Rapp. proc. verb. Renn., **56**: 1.
1930. Scr. utg. av det Norske vid. Akad. Oslo, I Mat.-nat. Kl., **5**.

Gran, H., and Birgithe. 1926. Avh. utg. av det Norske Urden.-Akad. Oslo, I Mat.-nat. Kl., **6**.

Hardy, A. 1925. Fish. invest., Ser. 2, **8**: 7.

Heinrich, K. 1934. Int. Rev. ges. Hydrobiol. and Hydrogr., **30**.

van Hille, J. 1938. Rec. trav. botan. néerl., **35**.

Hutchinson, G. 1942. Recent advances in limnology.

Janish, E. 1927. Das Exponenzialgesetz als Grundlage einer vergleichenden Biologie.

Jenkin, P. 1930. Int. Rev. Hydrobiol., **24**: 1–2.

Juday, Ch. 1940. Ecology, **21**.

Juday, Ch., and H. Schomer. 1935. Biol. bull., **69**: 1.

Ivlev, V. 1934. Biochem. Zt., **275**: 1–2.
  1939. Int. Rev. ges. Hydrobiol. und Hydrogr., **38**.
  1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven. 302 p.

Karsten, G. 1918. Zt. Botan., **10**.

Krys, A., E. Christensen, and A. Krogh. 1935. J. mar. biolog. assoc. Unit. Kingdom, **20**: 2.

Kreps, E., and N. Verjbinskaia. 1932. J. du Cons., **7**.

Kreutner, W. 1934. Arch. für Hydrobiol., **27**: 1.

Krogh, A., and E. Lange. 1931. Int. Rev. ges. Hydrobiol. und Hydrogr., **26**.

Kylin, H. 1916. Svensk. Botan. Tidskr., **10**.

Larsen, K. 1936. Rep. Dan. biolog. Stat., **41**.

Lindeman, R. 1941. Amer. midl. nat., **21**.
  1941a. Ibid., **26**.
  1942. Ecology, **23**: 4. (Translated in Usp. sovr. Biol., 1943, **16**: 5.)

Lotka, A. 1925. Elements of physical biology.

Lundbeck, J. 1926. Arch. für Hydrobiol. Suppl., **7**.

Marshall, S., and A. Orr. 1928. J. mar. biol. assoc. N.S., **15**.

Matsui, I., and S. Oshima. 1935. J. imp. fish. exp. Stat., **6**.

Maucha, R. 1924. Verhandl. intern. Ver. Limnol., **2**.

Mitscherlich, E. 1925. Die Bestimmung des Düngerbedürfnisses des Boden.

Moore, W. 1941. Ecology, **22**.

Moore, B., E. Prideau, and V. Herdman. 1915. Proc. and trans. Liverpool biol. soc., **29**

Needham, J. 1931. Chemical embryology.

Oppenheimer, K. 1921. Der Mensch als Kraftmaschine.

Petersen. 1926. Amer. j. sci., **7**.

Pfül, W. 1925. Gegenbaurs morph. Jahr., **54**.

Pirson, A. 1937. Zt. für Botan., **31**.
  1939. Planta, **29**.

Printz, H. 1926. Scr. utg. av. det Norske vid. Akad. Oslo, I Mat.-nat. Kl., **5**.

Pütter, A. 1924. Pflüger's Arch., **205**.

Rickett, H. W. 1920. Science, **52**.
  1922. Trans. Wis. acad. sci., arts, let., **20**.
  1924. Ibid., **21**.

Riley, G. 1940. Ecolog. monogr., **10**.

Rohberg, M. 1930. Jahr. für wissensch. Botan., **72**.

Rubner, M. 1902. Die Gesetze des Energieverbrauchs bei des Ernährung.
  1906. Arch. für Hyg., **57**.
  1908. Ibid., **66**.

Ruttner, F. 1926. **Planta, 2.**

Ruttner, F. 1926. Int. Rev. g

Scholz, K. 1933. Zt. für Fisch.

Schomer, H. 1934. Ecology, 15

Schreiber, E. 1927. Wiss. Me

Seiwell, H. 1934. Rap. in phy

Slobodkin, L. B. 1962. Energy
  Press, New York.)

Smith, F. E. MS, 1955. A restu
  27–32 *in* "Lectures on populat
  graphy, La Jolla, California.

Ström, K. Münster. 1932. Scr

Tamija, H. 1932. Acta Phytoch

Tangl, F. 1903. Pflüger's Arch.

Tansley, A. 1935. Ecology, **16**.

Terroine, E., et R. Wurmser.

Terroine, E., R. Bonnet, et R.

Thienemann, A. 1926. Zoolog.
  1931. Arch. für Hydrobiol.

Thimann, K., and Ch. Schneider

Volterra, V. 1933. Leçons sur
  1937. Acta biotheoret., **8**:

Waksman, S. 1941. Symposium

Waksman, S., and C. Carey. 19

Waksman, S., and C. Renn. 193

Walter, E. 1928. Richtlinien zu

Welch, P. 1935. Limnology.

vergleichenden Biologie.

e University Press, New Haven.

biolog. assoc. Unit. Kingdom,

nd Hydrogr., 26.

43, 16: 5.)

sses des Boden.

tra. Liverpool biol. soc., 29

at.-nat. Kl., 5.

Ernährung.

Ruttner, F. 1926. Int. Rev. ges. Hydrobiol. und Hydrogr., 15.

Scholz, K. 1933. Zt. für Fisch., 30.

Schomer, H. 1934. Ecology, 15: 2.

Schreiber, E. 1927. Wiss. Meeruntersuch., Abt. Helgoland., 16: 10.

Seiwell, H. 1934. Rap. in phys. oceanogr. and meteorol., 3: 1.

Slobodkin, L. B. 1962. Energy in animal ecology. Advances Ecol. Res., 1: 69–101. (Academic Press, New York.)

Smith, F. E. MS, 1955. A restudy of the Lindeman approach to community dynamics. Pages 27–32 *in* "Lectures on population dynamics", multigraphed by Scripps Institution of Oceanography, La Jolla, California.

Ström, K. Münster. 1932. Scr. utg. av det Norske vid. Akad. Oslo, I Mat.-nat. Kl., 3.

Tamija, H. 1932. Acta Phytochim., 6.

Tangl, F. 1903. Pflüger's Arch., 98.

Tansley, A. 1935. Ecology, 16.

Terroine, E., et R. Wurmser. 1922. Bull. soc. chim. biol., 4.

Terroine, E., R. Bonnet, et R. Duquenois. 1927. Ibid., 9.

Thienemann, A. 1926. Zoolog. Anz. Suppl., 2.
1931. Arch. für Hydrobiol., 22.

Thimann, K., and Ch. Schneider. 1938. Amer. J. botan., 25.

Volterra, V. 1933. Leçons sur la théorie mathématique de la lutte pour la vie.
1937. Acta biotheoret., 8: 1.

Waksman, S. 1941. Symposium in hydrobiology.

Waksman, S., and C. Carey. 1935. J. bacteriol., 29: 5.

Waksman, S., and C. Renn. 1936. Biol. bull., 60: 3.

Walter, E. 1928. Richtlinien zur Karpfenfütterung.

Welch, P. 1935. Limnology.

[Thesis portion]

FACTORS INFLUENCING TROUT PRODUCTION IN FOUR MOUNTAIN IMPOUNDMENTS IN CENTRAL EASTERN ARIZONA

Phillip A. Stewart

Table of Contents and Abstract from Master of Science Thesis
Arizona Cooperative Fishery Unit
THE UNIVERSITY OF ARIZONA

1967

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF ILLUSTRATIONS

ABSTRACT

Photosynthesis of plankton and benthos (in situ), standing crops of chlorophyll and zooplankton, and plant nutrient income from tributaries were measured at 4 mountain lakes in central eastern Arizona between August 1965 and August 1966 to determine their relation to game fish production. Standing crop of zooplankton was considered the most reliable available index of secondary production. Despite high benthic photosynthesis at 2 lakes, phytoplankton appeared to be the principal support for zooplankton. The possibility must be considered, however, that energy from benthic plants may pass through benthic fauna and not zooplankton. High zooplankton standing crop relative to phytoplankton photosynthesis at Becker Lake was attributed to the comparatively shallow mean depth. Alkalinity and phosphate were the only two chemical factors related to phytoplankton photosynthesis. Physical factors (water clarity and average depth) were more important than chemical factors in determining benthic photosynthesis. To improve standing crop of chlorophyll as an index of phytoplankton photosynthesis, a method of relating assimilation number to euphotic depth is presented.

836 Wood
Ft. Collins, Colorado 80521
May 19, 1969

Mr. Wiegand
Room 318, Liberal Arts Building
Colorado State University
Ft. Collins, Colorado 80521

Dear Mr. Wiegand,

This report on prospective salmonid fish introductions in Western North America is hereby submitted in accordance with your assignment.

The report includes ecological data on several salmonids, an analysis of each one, and conclusions and recommendations of the author.

Sincerely yours,

James L. Hicks

JAMES L. HICKS

Enclosure

JLH/fr

REPORT
ON
PROSPECTIVE SALMONID
FISH INTRODUCTIONS IN
LAKES OF WESTERN
NORTH AMERICA

[illegible]

Submitted to
Mr. Wiegand
Professor of Technical Journalism
Colorado State University
Ft. Collins, Colorado

by
James L. Hicks
Wildlife Biology Student

May 19, 1969

↓1¼"

ABSTRACT

The purpose of the study was to consider the introduction of some salmonid fishes for the purpose of increasing the sport fishery potential in large, cold water lakes of Western North America, with particular emphasis on Colorado.

Research of written material was the main technique used in this report. The personal advice and couseling of Robert Behnke of the Colorado Cooperative Fishery Unit was very valuable.

The conclusion is that a new, more pre-adapted sport fish is needed for the many large bodies of water being produced, because the sport fishes presently being used are not successful from a fishery management standpoint.

It is recommended that further study and experimentation be carried out on the salmonids of this report, and intra-specific variations of salmonids presently being stocked, to find the best species or intra-specific variation to introduce that would improve the sport fishing potential of a lake.

TABLE OF CONTENTS

Rewrite
type

no

PROSPECTIVE SALMONID
FISH INTRODUCTIONS IN
LAKES OF WESTERN
NORTH AMERICA

INTRODUCTION

Purpose

The purpose of the study was to consider the introduction of some salmonid fishes for the purpose of increasing the sport fishery potential in large, cold water lakes of Western North America, with particular emphasis on Colorado. Some biological considerations, growth rate, food diet, spawning habits, life span, habitat, and intra-specific variation, of several exotic salmonid species are related to that niche they may fill when introduced into new waters.

Particular importance was put on intra-specific variation, and its implications to fishing management. The more effectively an ecological niche is filled in the lake environment, the easier it will be to maintain a sport fish population, and increase its yield.

Significance

Originally, there were very few natural lakes in Colorado, and in many parts of Western North America. Background

1¼"

For this reason there were very few native "game" fish (only cutthroat trout and Rocky Mountain white-fish in Colorado). Today, with the great increase in reservoir construction, a vast new environment has been created. The native species have virtually disappeared because they could not adapt to this new environment. Consequently almost all of Colorado's sport fishes are non-native introductions. These introductions have not been fully successful from a management standpoint.

Background

The two main lake introductions are the rainbow and brown trouts. Both are extremely good sport fish. The rainbow typically are not as successful as brown trout in maintaining a wild population, and must be continuously stocked, but are cheaper to raise and easier to catch. Brown trout typically are difficult to catch, but will maintain a wild population.

Intra-specific variability is taking on increasing significance for fishery management as more is learned about it, and the information on intra-specific variations (within a species) of fish becomes available, and suggests real potential as a management tool.

Natural selection is the driving force responsible for changes in population gene pools. Natural selection produces the best adapted genotype for a specific environment. In nature this process is

1¼"

extremely slow, but very effective. This genetic variability produced in populations in different geographical areas holds a real and virtually untapped potential for fishery management purposes. The goal is to fit the best adapted genotype to the different conditions it is best suited for.

Scope

The scope of the study was limited to the sub-family Salmoninae, and the species considered to have the most potential for introduction in large, cold water lakes of Western North America. The report was written for fishery biologists to acquaint them with the potential of these salmonids, references for further information, and the importance of intra-specific variability in fishes. The salmonids discussed are: *Salmo letnica*, *Brachymystax lenok*, *Oncorhynchus kisutch*, *Orchorynchus nerka*, *Salvelinus malma*, *Salvelinus alpinus*, *and Hucho*, *Salmo marmoratus*.

↓1¼"

Definitions

All Flush IV Readings

Anadromous--going up river from sea to spawn.

Benthic--area of lake at the deep bottom.

Crustaceans--class of Arthropoda, including shrimps, crabs, and water fleas.

Cypinids--minnows, carps, and other forage type fish.

Fluviatite--fish living or growing in streams.

Genotype--genetic differences within a species producing races, or strains with different internal characteristics but not always external differences.

Intra-specific variability--characteristic differences amongst members of the same species through natural selection.

Littoral--area of lake near shore; sub-littoral is zone next to littoral out from shore.

Pelagic--Inhabiting the mass of water of a lake, in contrast to the lake bottom, and away from shore.

Plankton--Animals and plants of a lake which float or drift almost passively; near the surface of the lake.

Sub-lacustrine zone-- bottom of lake along the shore.

↓1¼"

INVESTIGATION

Method of Survey

The major portion of the information in this report was taken from numerous sources of written information, including many translated reports from Europe, and reports and books from agencies in the United States. This information was also supplemented with the personal knowledge of Robert Behnke, Assistant Unit Leader of the Colorado Cooperative Fishery Unit.

Data

Salmo letnica. The Lake Ohrid Trout, is a relict form of pre-glacial freshwater trout, and originally was found only in Lake Ohrid on the Yugoslavian-Albanian border. Lake Ohrid is the oldest lake in Europe.

Salmo letnica is made up of three intra-specific races, typicus or Pestani trout, aestivalis or Summer trout, and balcanicus or Struga trout. Each race has a separate spawning area and season.

Such a situation is ideal from a fishery management point of view because constant year-round recruitment is attained. Races of letnica probably have diverged within Ohrid itself and have a very long history of lake adaptation.

✓ 1¼"

≡

The growth rate of letnica in Lake Ohrid is moderate. The Struga race has the fastest growth rate and reaches an average of 18 inches in five years (A-1). Pestani reaches an average of one pound in seven years (A-2).

The diet of the Ohrid trout is rather monotonous in comparison with other large salmoids. sp No diet information is available for the Summer trout. The main food elements are cyrinid fishes (minnows), and planktonic crustaceans. The benthic fauna elements in the diet are mainly crustaceans of the orders Amphripoda and Osopoda, and predominatly sp forms which live in the littoral and sub-littoral zones.

Salmo letnica that is less than 40 cm (15 inches) feed almost completely on plankton. Those over 40 cm change more to a fish diet. During the spring, fall and spawning season the adult letnica stays in the littoral zone where it feeds intensively on fish. During the summer it emigrates to the deeper central layers of the lake where it feeds partly on plankton (A-3).

The large percentage of empty stomachs in the winter months is due to the spawning seasons. A high percentage of spawn in their diet at certain times may be noteworthy because it shows they eat their own spawn.

1¼"

The Cyprinids *Alburnus albidus scoranzoides* makes up 88% of letnica's fish diet. This is because Alburnus is the most numerous species of fish in the lake.

The Ohrid trout is selective in its plankton diet, feeding almost exclusively on the *Daphina pulex* (water flea). *Daphina pulex* is also common in the plankton form in lakes of North America.

Struga and Pestani are sexually mature at the end of their fifth year. The Summer race usually attains sexual maturity at the end of the fourth year.

Each race has a different spawning ground and spawning seasons, and because of this each race represents a genuinely isolated reproductive community. Struga, the largest of the three, spawns in December predominantly along the northwest shore in the lake sand and in running water at the influx of the river. Pestani race spawns in January and February in a distinct spawning ground along the eastern shore, in the vicinity of sub-lacustrine zones. The summer race spawns in sub-lacustrine zones along another area of the eastern shore from May to July.

Salmo letnica evolved in Lake Ohrid over many thousands of years; and is completely suited for this type of environment. The commercial fish population of the lake is made up of 45% Salmonids (mostly letnica),

↓1¼"

40% Cyrinids fish, and 5% Eel. Lake Ohrid is similar to many large cold water lakes in Colorado. (1)

Salmo letnica is closely related to the brown trout, Salmo trutta, and very similar in feeding habits and behavior. Possible advantages of letnica are constant recruitment with three races present, a long history of lake adaptation, and being more susceptible to angling than the brown trout. All these factors suggest very strongly that letnica may have a valuable fishery potential for introduction into lakes and reservoirs of North America. Letnica is of particular interest because it will be introduced into Colorado lakes this summer, and its outcome may prove valuable.

ECOLOGY OF RACES OF SALMO LETNICA

Race	Spawning Time + Place	age at 1st Spawning	max. age + Avg. Growth	Food Habits + % Commercial catch
Struga	December Lake Sano Running water at inlet	End 5th year	Recorded to 7 years avg. 18in. in 5 yrs.	25% Cyprinid Fish 25% Plankton Daphina pulex 44% Empty all 3 Races make up 45% Fish catch
Peštani	Jan. Feb. Sub-lacustrine zones	End 5th year	Recorded to 7 years avg. 14in. in 5 yrs.	Same
Summer	may to July Sub.-lacustrine Zones	4th year	Recorded to 7 years avg. 15in. in 5 yrs.	Same

(1)

Table 1

↓ 1¼"

Oncorhychus Kisutch. The silver or coho salmon of the Pacific Ocean is a supurb game fish and a superior food fish. It holds promise for large cold lakes with an abundant supply of forage fish, insects, amphipods, and large crustaceans.

Coho salmon reared in lakes usually do not spawn successfully; so the fishery must be maintained by fish hatcheries. The establishment of freshwater brood stock by selective breeding is one possibility of developing a population of coho that would maintain itself. One strain was reared for three generations in California hatcheries before a disease outbreak ended the experiment. The fish matured in their second and third years, lost their natural spawning instinct, and produced larger, more delicate eggs (2).

Growth of coho salmon in the Pacific Ocean is extremely rapid. In the short period of 18 months, they increased in size from less than an ounce to an average weight of nine pounds. This growth was actually exceeded when coho were planted in Lake Michigan. The reason for this exceptional growth is the type of food supply. In the Pacific they have large quantities of small forage fish, and in Lake Michigan they can feed heavily on alewifes, a small freshwater herring. This type of food supply is rarely found in North American lakes.

↓1¼"

Coho salmon add a great deal of variety to the sport fishery. In the young stages they feed near shore and provide excellent fishing. But they do not have the long life span of the rainbow trout (3).

Although fabulously successful in Lake Michigan, the Coho is not the universal salmonid sport fish for all waters. Recent reports on coho stocked in two Colorado lakes show that growth was about the same as rainbow trout, with the disadvantage of a short life (4). In smaller impoundments without abundant forage available, rainbow and brown trouts can be expected to provide better results.

Onchorynchus nerka. The Kokanee salmon is the nonandromous form of the sockeye salmon. O. nerka has many strains or races, and each with different characteristics. It is important to understand these different characteristics in order to match strains with the water to be stocked.

The Kokanee completes its life cycle entirely in freshwater. The life cycle varies, depending on latitude and elevation, between two and seven years. They die after spawning. They spawn depending on race from August to January.

A suitable lake for Kokanee should be deep, with much shore area, and a water temperature close to 50° F. Kokanee spawn in tributaries and outlets to a

↓1¼"

≡

lake, or in suitable shoreline gravels in the lake itself. It is suspected that strains may differ in their ability to spawn in lakes, although this is not proven yet.

The average growth rate is typically 9 to 14 inches in five years depending on the waters. Kokanee is not very predacious, and feeds primarily on pelagic zooplankton (5, 14).

Kokanee have value as forage fish in only a few lakes. They also make a good game fish to supplement the rainbow in some lakes.

Brachymystax lenok. This little known species is found in all rivers of Siberia to the Sea of Japan. It never descends to salt water. B. lenok spawns in May and June. It has a moderate growth rate, but a long life span of over twelve years. Its length goes up to 670 mm (22.5 inches), and weighs from three up to 8 and 10 pounds. B. lenok feeds on larvae and adult insects, amphipods, small fish, frogs, mice, and salmon spawn. B. lenok has not been introduced outside its native range, and there is only sparse data in the literature concerning life history and ecology (6,7,8).

3

consistency

Salvelinus malma. The Dolly Varden clarr is native to both sides of the Pacific Ocean from Japan to California, and consists of many intra-specific populations with anadromous, lacustrine, and fluviatite forms.

↓1¼"

Dolly Varden reach maximum sizes of 5 to over 15 pounds in various localities, but adults usually average one-half to several pounds. Their feeding habits are similar to trout. They are reputedly voracious fish eaters, but evidence does not support this. Armstrong (9) prepared a useful bibliography on the Dolly Varden.

Salvelinus alpinus. The Artic charr is holoartic in distribution, and very closely related to the Dolly Varden charr. The average length of winter charr found in the USSR by Berg was 535 mm (22 inches) and the weight ranged between three and eight pounds up to 15 pounds. The spring form is slightly smaller.

The artic charr spawns in the fall. There is an opinion that the Novaya Zemlya charr winter in deep lakes. The life of this fish has been recorded in Russia up to eight years with a length of 22 inches. Seven and eight year old specimens are dominant in the catches.

The Artic charr consists of many intra-specific forms with very different ecologies and life histories. For further information see (6,10,11,12).

Hucho. The genus Hucho consists of probably four species. They are large, predatory, pike-like salmonoids. The most important species are H. hucho of the Danube basin, H. taimen of Siberia, and H. perryi from northern Japan.

1¼"

Hucho reaches a relatively enormous size, up to more than 100 pounds. Their life span is often over 20 years. According to Svetina the average weight is over 13 pounds, and 34 inches at seven years. They usually spawn in April.

consistency

Because of their large size, predatory habits, and long life span, they may have potential as an introduction. Hucho hucho was transplanted of the Atlas Mountains of Morocco in 1952, and are successfully reproducing.

Berg (1948) discusses the systematics and some biological data of these three species (6). Svetina (1962) prepared an FAO synopsis on the biology of Hucho hucho (13).

Salmo marmoratus. This is a large, predaceous trout native to Adriatic tributaries in northern Italy and Yugoslavia. It is known to attain a weight of more than 50 pounds and is a highly prized sport fish in its native waters. It has not been introduced outside its native range as yet, but a recent publication (15) presented data on its ecology and culture which should encourage experimental introduction.

↓1¼"

ANALYSIS

Food availability is the key to fish growth and reproduction. This should be the prime consideration in managing a lake for sport fishing. The purpose of introducing new game fish is to utilize the food supply better. That is to get more poundage of fish out the same waters by filling a niche that is not filled. This can be done in several ways.

In the case of the kokanee, an introduction can more effectively utilize food in the environment not being used by other game fish, thus not effecting other fish, but providing another game population.

In lakes where the trout are not doing well and rainbow must be introduced on a put-and-take basis, a fish like Salmo letnica or a intra-specific race of rainbow or brown could be introduced that would be able to maintain a wild population and improve fishing.

In waters where over population of undesirable "trash" fish or a stunted population of brook trout is present, a large predatory fish such as the Hucho, S. marmoratus, S. malma or the Coho salmon could provide a good sport fishery by feeding on these forage fish. In some cases the forage fish may be competing too heavily with the rainbow trout and thus not letting it grow and reproduce properly.

1¼"

Each of the salmonids discussed hold potential for improving present sport fishing conditions in large, cold water lakes; but where and how it will be useful depends on the conditions of the lake.

Every aspect of <u>Salmo</u> <u>letnica</u> indicates that it should be successful in lakes similar to Lake Ohrid. It's feeding habits, the type of food, are consistent with the foods and feeding habits of brown and rainbow trouts in North America. The Lake Ohrid trout goes beyond the rainbow because it is able to maintain a wild population. Its long history of lake adaptation, and proven success as a lake spawner gives it great potential for being able to maintain itself. If all three races of letnica were introduced, there would be year-a-round recruitment in case one population failed.

<u>S.</u> <u>letnica</u> also goes beyond the brown trout, in its potential as a game fish, because it is more susceptible to angling by the fisherman. Needless to say this is the main problem with the brown trout being used in Colorado.

A long background of lake adaptation, and lake spawning along with being more susceptable to angling give <u>letnica</u> the highest potential for experimental introductions.

<u>O</u>. <u>Kisutch</u>, the coho salmon, although fabulously successful in Lake Michigan, is not the universal

↓1¼"

slamonid sport fish for all waters. In smaller impoundments without abundant forage available, rainbow and brown trouts and kokanee slamon can be expected to provide better results. The coho salmon would be useful in lakes where there is a large population of pelagic forage fish.

The main value of the kokanee (_O_._nerka_) is as a supplemental sport fish which makes more efficient utilization of the total environment because it prefers different water strata and food. Because there is not much competition with other trout species, a higher total poundage and numbers of salmonid fishes can be produced in a lake with kokanee and mixed trout species.

More numerous and more fully developed gillrakes allow straining of minute food items from water which are not available to rainbow trout and other species of trout.

In some lakes such as Lake Pend, O'reille, Idaho, the kokanee provides valuable forage for predatory trout and the great size attained by rainbow trout of this lake is attributed to kokanee forage.

Salvelinus _malma_, Dolly Varden charr, has a questionable potential for introduction. In Alaska where it is very common, it is considered with disdain; however, it is a good food and game fish, and has a

1¼"

potential perhaps for introduction into cold,high mountain lakes with stunted brook trout (Salvelinus fontinalis) populations. Under these conditions the more predatory nature of the Dolly Varden may produce a better quality fishery yielding larger trout. Dolly Varden charr from Alaskan stock were distributed in 1968 to Colorado, New Mexico and Utah for experimental introductions.

The Artic Charr consists of many intra-specific forms with very different ecologies and life histories. Except for some relict populations such as the Sunapee charr and the blueback charr of New England and the Alpine charr of Europe, this species has not been widely introduced to new waters. Considering the wealth of diversity possessed by this wide ranging species, there is a strong suggestion of a valuable potential for fish management purposes.

Hucho because of its large size, predatory habits, and long life span may have potential in large rivers where cyprinid fishes are not providing good sport fishing and may fill the need for a large preditor. sp Hucho taimen inhabits cold lakes of Siberia. Sventina (1962) recommends Hucho be introduced into cyprimid waters~~,~~ below the trout zone in large rivers. This would suggest Hucho has great variety for different conditions~~,~~ within it.

↓1¼"

Brachymystax lenok. This Siberian trout is mainly an invertebrate feeder in large, cold rivers and lakes. Little is known of its ecology and potential for introductions into new waters, but it appears to be a highly desirable sport fish and should be investigated further.

Intra-specific variability within more common species, such as the rainbow and brown trouts, is also an important consideration to regard in finding a new fish to improve the sport fishery. The great challenge of fishery management is to utilize pre-adapted, intra-specific variability to maximize the potential of a sport fishery.

Often within a species, strikingly different results can be obtained; for example, Kamloops rainbows when stocked with hatchery rainbows in a large lake with minnows and suckers present will become very predaceous early and grow and survive at tremendous rates, surpassing the hatchery rainbow (2).

CONCLUSIONS

1. The main sport fish (rainbow and brown trouts) presently being stocked in Colorado and most large, cold water lakes of the west are not completely successful from a fishery management standpoint. Rainbow trout of the fish hatchery type are stocked on a

↓1¼"

put-and-take basis and will not establish a natural population under fishing pressure. Brown are difficult to catch.

2. Intra-specific variability holds the potentail of providing specific races of a species better suited for growth and reproduction in a certain environment.

main conclusion (should be first)

3. There is a need for new game fish species, or intra-specific variation of a species presently being used, to be introduced into the large reservoirs, that will prove more efficient in providing a sport fishery under increased fishing pressure.

4. The salmonids discussed within the report have specialties that can be useful to fishery management to increase sport fishing in large, cold water lakes of Western North America.

RECOMMENDATIONS

1. In lakes where the sport fishing is fair to good, it is never recommended to tamper with the environment by introducing a new fish.

2. In lakes where the sport fish are not doing well because of competition from forage fish or because overpopulation is causing stunted fish, it is recommended that a large predacous fish such as *Hucho*, *Salmo marmoratus* or *S. malma* be introduced depending on the specific conditions.

↓1¼"

3. In lakes where an additional game fish is needed to provide more fishing, the Kokanee salmon <u>O. nerka</u> should be introduced.

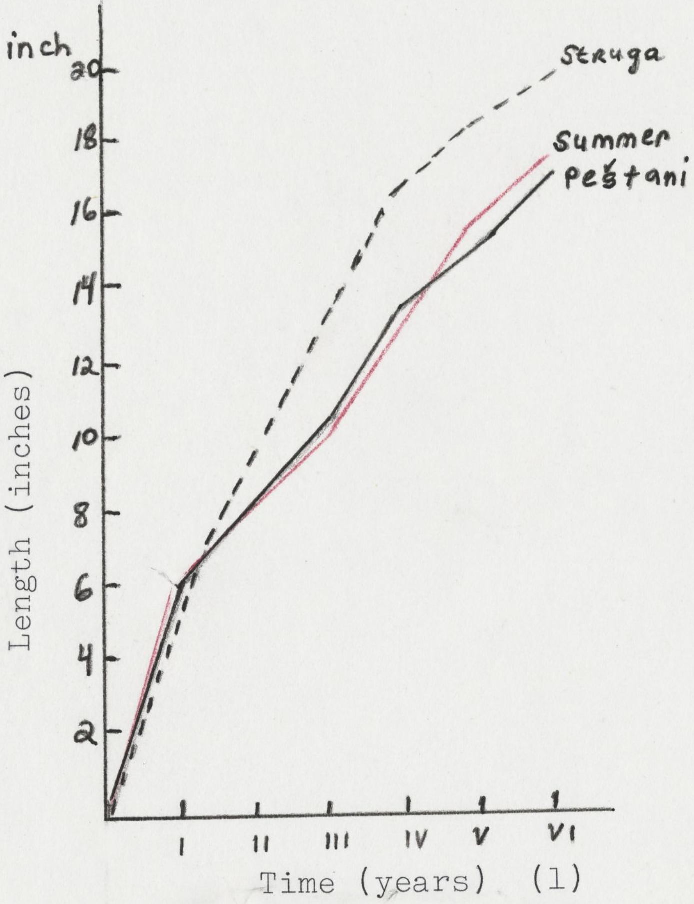
4. In lakes where the present sport fish population is not maintaining itself and being stocked on a put-and-take basis or is too difficult to cath and not providing sufficient fishing, it is recommended that a possibly better, pre-adapted fish such as <u>Salmo letnica</u> or a intra-specific variation of the rainbow or brown trouts be introduced.

First 5. The major recommendation is for further study to be done on the salmoids discussed in this paper and other possible game fish that would be useful in fishery management. 2d It is also recommended that more study be done in the hardly touched field of intra-specific variations within species of fish, because it has unlimited potential for providing better fishery management.

APPENDIX A

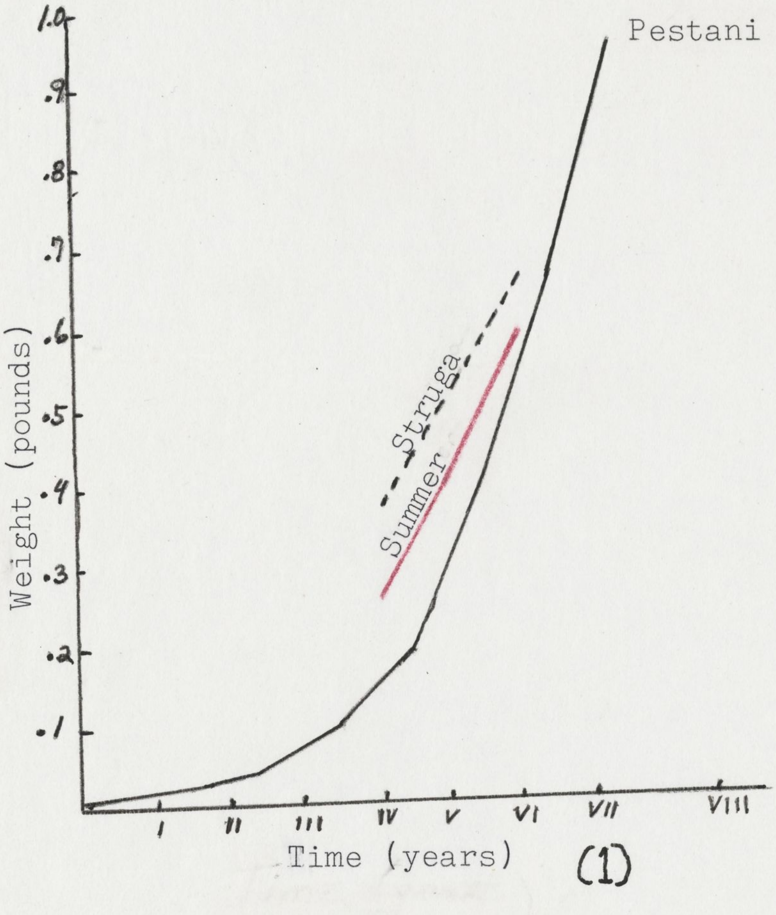
A-1

GROWTH RATE OF <u>SALMO</u> <u>LETNICA</u> [illegible]



Graph 1

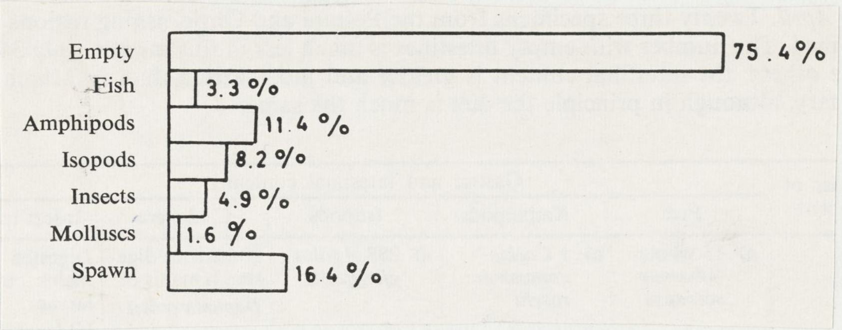
WEIGHT GROWTH OF <u>SALMO</u> <u>LETNICA</u> caps & lc



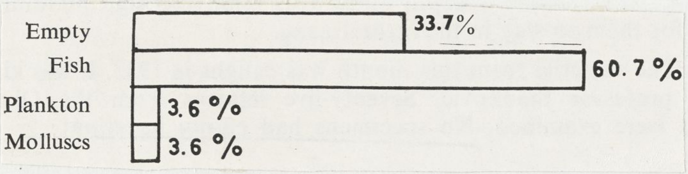
Graph 2

MONTHLY DIET OF <u>SALMO</u> <u>LETNICA</u> [illegible]

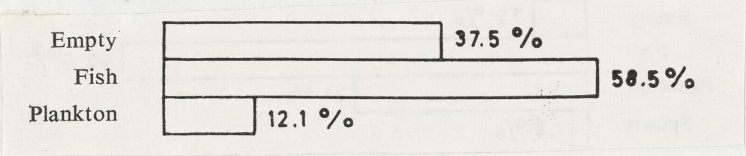
January (Winter)



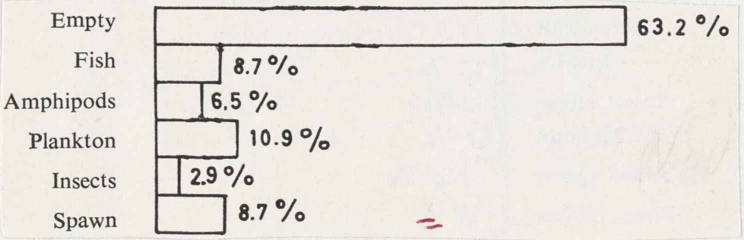
May (Spring)



July (Summer)



November (Fall)



Graph 3

(1)

ACKNOWLEDGEMENTS

To Mr. Robert Behnke of the Colorado Cooperative Fishery Unit for his help in this report.

To Mrs. F. Roberts for her typing help.

BIBLIOGRAPHY

1. Stefanovic, Dusica. Racial and Ecological Study of the Ohrid Salmonids, trans. Paul Pignon. Washington, D. C.: Department of Interior, 1966. w

2. Calhoun, Alex ed. Inland Fisheries Managment, ed. Alex Calhoun. State of California, Dept. of Fish and Game, 1966.

3. Tody, Wayne H., and Howard A. Tanner. Coho(silver) Salmon for the Great Lakes. State of Michigan, Dept. of Conservation, 1966.

4. Klein, W. D. and L. M. Finnel. "Comparative Study of Coho Salmon Introductions in Parvin Lake and Grandby Reservoir," Progressive Fish-Culturist, XXXI, #2 (April, 1969), 78-108.

5. Seeley, Charles M. and George W. McCammon. A Review of Kokanee In California. Report California Dept. of Fish and Game. Inland Fisheries Administration Report # 63-11, 1963.

6. Berg, Leo S. Freshwater Fishes of the U.S.S.R. and Adjacent Countries, lc Trans. Omry Ronen. Jerusalem: Israel Program for Scientific Translations, 1962.

7. Kirillov, F. N. The lenok Brachymystax lenok. USSR: Hauchnye Soobshcheniya, ~~Vol. 1~~ I, 1958.

8. Podlesnyi, A. F. Brachymystax lenok. USSR: Trud. Vsesoyus, 1953.

9. Armstrong, R. H. Annotated Bibliography on the Dolly Varden Charr. Juneau: Alaska Dept. of Fish and Game, 1965.

10. Grainger, E. H. The Artic Charr of Frobisher Bay. Canada: Journal of Fishery Resources, 1953.

11. Savvaitova, D. A. Intra-specific Forms of Salvelinus alpinus. USSR: Vopr. Ikhtiol, 1961.

12. Quartier, A. Biology of the Salvelinus alpinus in Lake Neuchatel. France: Suisse Zool. ab 1951.

13. Svetina, M. *FAO Snyopsis on the Biology the Hucho*. Rome: European Inland Fisheries Advisory Commission, 1962.

14. Chapman, D. W. R. J. Cambell and J. D. Fortune. *Kokanee and Trout in Elk Lake*. Trans. American Fishery Society, 1967. lc

15. Sommani, E. "*Salmo marmoratus* in Northern Italy," *General Fisheries Council for the Mediterranean*, ed. Rome: FAO, 1961.

These should be in alphabetic order

Made in th[illegible]ed States of America
Reprinted from TRANSACT[illegible] THE AMERICAN FISHERIES SOCIETY
Vol. 10[illegible]5, September 1977
© Copyright by the American Fisheries Society, 1977

SH
1
A51
106:5
1977

Survival, Growth, and Prey of Esocidae in Experimental Systems

A. STEPHEN WEITHMAN AND RICHARD O. ANDERSON

Missouri Cooperative Fishery Research Unit[1]
University of Missouri, Columbia, Missouri 65201

ABSTRACT

Survival (July to November) of young-of-the-year esocids stocked in 0.2-hectare experimental ponds in Missouri was: muskellunge (*Esox masquinongy*), 24%; northern pike (*Esox lucius*), 58%; and the F_1 hybrid of these two species (commonly called the "tiger muskie"), 74%. Survival of yearlings from April to September was: muskellunge, 80%; northern pike, 90%; and hybrids, 85%. Growth rate of yearlings of all three forms was rapid in late spring, declined to a seasonal low in July, and then increased until the ponds were drained in September. Average weight gain of the hybrids (719 g) during their second year of life in ponds was significantly greater than that of northern pike (617 g) or muskellunge (615 g). Maintenance diets (grams of food per gram of fish) calculated for fish in tanks (1.2 × 4.8 × 1.1 m) for 28-day periods were as follows: northern pike, 0.23; muskellunge, 0.51; and hybrids, 0.62. Food conversion efficiencies in tanks were: northern pike, 29.0%; muskellunge, 25.0%; and hybrids, 22.0%. Non-game species were more vulnerable than game fishes to esocid predation in tanks. An esocid can be stocked in addition to or as an alternative to largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion v. vitreum*), or striped bass (*Morone saxatilis*) because of a faster rate of growth. The hybrids may be the most desirable form of the three esocids because of rapid growth rate, intermediate angling vulnerability, and ease of rearing in a hatchery compared to either parent species.

Fish communities of some midcontinental reservoirs contain appreciable densities of underused adults of non-sport species such as gizzard shad, *Dorosoma cepedianum* (Buss 1960). The goal of enhanced fishery benefits can be achieved by using prey species to support a fishery for predators. The stocking of predator fish may result in better balance in fish communities and improvement in the quality of fishing. Large piscivorous fishes, such as striped bass (*Morone saxatilis*), walleye (*Stizostedion v. vitreum*), and pikes (Esocidae) have been introduced into reservoirs for these purposes.

The goal of the present study was to determine if there is a biological advantage in stocking northern pike (*Esox lucius*), muskellunge (*Esox masquinongy*), or the F_1 hybrid of these two species (here termed "hybrid"; commonly called the "tiger muskie" by fishermen). Survival, food conversion efficiencies, growth rates, and vulnerability of prey species were compared and stocking recommendations proposed.

METHODS

Tank Experiments

All experiments were conducted at the Little Dixie fishery research area, 21 km east of Columbia near Millersburg, Missouri. Consumption, growth rates, and efficiency ratios were derived from data from a set of experiments conducted in concrete tanks (1.2 × 4.8 × 1.1 m with a volume of 6.3 m^3). Water from Little Dixie Lake was continuously exchanged at the rate of about 95 liter/min. Turnover time was about 1 hour. Cover screens of 2.5-cm mesh wire were fitted for all tanks to prevent fish from jumping out and to avoid predation by birds. Temperature was recorded with a maximum-minimum thermometer three times a week.

The tanks were divided into two equal units by center screens (0.95-cm mesh). One predator was introduced into each unit. The study was conducted with a total of nine fish—three northern pike, three muskellunge, and three hybrids. All fish were age I and initially ranged from 262 to 285 mm long (all length measurements used herein refer to total lengths). Growth and food consump-

---

[1] A cooperative program of the U.S. Fish and Wildlife Service, Missouri Department of Conservation, and University of Missouri–Columbia.

American Fisheries Society
ORGANIZED 1870 | INCORPORATED 1910

RICHARD H. STROUD
PRESIDENT 1979-1980

CARL R. SULLIVAN
EXECUTIVE DIRECTOR

ROBERT L. KENDALL
EDITOR

January 29, 1980

Mr. R. Max Peterson, Chief
Forest Service
U.S. Department of Agriculture
12th and Independence Avenue, S.W.
Washington, D. C. 20250

Dear Max:

The American Fisheries Society is concerned about the Forest Service's management of riparian-stream ecosystems. We believe that the basic Forest Service philosophy on riparian management is essentially sound and that some of your land managers take many appropriate field actions to maintain, restore, and protect valuable riparian ecosystems. However, recent remarks and/or field instructions made by Forest Service administrative personnel regarding riparian ecosystems tend to cloud the issue. These misleading and, in our view, inappropriate statements represent roadblocks to proper management of national forest lands under the highly accepted principles of multiple-use and sustained yield.

Our concerns relate particularly to remarks made by Deputy Chief Dr. Thomas C. Nelson in a speech entitled, "The Forest Service Range Role as the 1980's Begin." The speech was delivered before the Range Ecology Working Group Panel at the Society of American Forester's 1979 Convention, Boston, Massachusetts, October 16, 1979. We find several of Dr. Nelson's remarks to be misleading in terms of the management of livestock grazing and the impacts on riparian-stream ecosystems. As you are aware, probably no other use of these riparian areas has received more criticism than livestock grazing. Many agencies (federal, state, conservation, and professional organizations) have demonstrated and documented that improper livestock grazing of riparian ecosystems is the major cause of reduced quality and productivity of fish and wildlife habitat. It is also the chief cause of deteriorated water quality and reduced instream flows. A recent Forest Service (Region 4) publication, <u>Riparian Wildlife Resume</u>, illustrates the concerns of the Service toward riparian zone management and the conflicts associated with livestock grazing. Dr. Nelson's speech does not convey these concerns.

Several sections of Dr. Nelson's speech are biased toward range management and contain misleading statements that if left to a myriad field interpretations by Forest Service personnel could adversely impact attainment of the enlightened range management which has been the goal of range, wildlife, and fisheries scientists. We understand, for example, that Region 4 has transmitted the speech to its field offices as "... important direction as to where range management should be headed in the 1980's..." As we will point out herein, some of Dr. Nelson's statements contradict statements made by former Forest Service Chief, John McGuire, at Calloway Gardens, Georgia, December 11-13, 1978, during the National Symposium for the Protection and Management of Floodplains, Wetlands, and Other Riparian Ecosystems. Many of Chief McGuire's remarks at that symposium addressed the livestock grazing and riparian management issues. For instance, he stated that, "It came as no surprise that livestock grazing has the greatest single impact on riparian areas in the Southwest and Intermountain areas." We understand that his remarks were based, in part, on findings of a Forest Service Riparian Habitat Task Force which finished its assignment in November 1978 prior to the Symposium. It is unfortunate that Region 4, which administers a large portion of the Intermountain area and is specifically mentioned as a problem, would transmit Dr. Nelson's speech to its field offices with no clarification. Chief McGuire also stated in Georgia, "But, policy is one thing. Interpretation and action on the ground can be another."

Dr. Nelson has stated that, "On the National Forests and National Grasslands, grazing allotments are managed in concert with other resource uses." We hope that someday this statement becomes a fact. Forest Service technical reports and national symposia proceedings, have pointed out that on-the-ground management of range and riparian resources are not being properly administered in terms of total resource values. National symposia and workshops have been built around these issues since 1974; the 1978 symposium Mr. McGuire attended in Georgia being an example. Other notable symposia have been the Symposium on Livestock Interactions with Wildlife, Fisheries, and Their Environments, Reno, 1977; USDA-FWS Seminar on Improving Fish and Wildlife Benefits in Range Management, Washington, D. C., 1976; Forum on Grazing and Riparian/Stream Ecosystems, Denver, 1978; Wild Trout I (1974) and Wild Trout II (1979) Symposium, Yellowstone National Park; and the Symposium on Importance, Preservation, and Management of Riparian Habitat, Tucson, 1977.

The aforementioned statement in Dr. Nelson's speech appears then to have been quickly contradicted by one shortly following which states that "... about 15 million acres of range land are in unsatisfactory condition." Dr. Nelson reiterates that, "A great deal has been said about the conflicts between wildlife and livestock, particularly in riparian zones. However, these are generally local problems and the degree of conflict is low." That problems are local and conflicts low are unsubstantiated, and misrepresent data presented in the meetings I have cited, as well as in Forest Service technical reports.

Dr. Nelson continues with the statement, "... under reasonable and sound livestock management, we can mitigate and resolve these problems. We have the knowledge to do so (emphasis added)." Certainly, the Forest Service knows what the problems and impacts are, but in most cases field managers are not exercising wise land management to arrest the continuing deteriorating conditions in Western rangeland riparian ecosystems. The cause of this continuing range deterioration must be addressed by developing compatible grazing systems which consider riparian ecosystem values.

Dr. Nelson's view that grazing will improve watershed conditions more than complete protection from grazing is not supported by the facts. The literature is replete with studies that demonstrate that grazed watersheds produce more sediment than ungrazed watersheds. It is almost axiomatic that grazed watersheds have a much higher count of fecal coliform and other bacteria in their waters than in the waters from ungrazed watersheds. Many studies have shown decreased fish populations in grazed vs. ungrazed areas; in fact, we are aware of no study which shows higher fish populations in grazed areas.

In his concluding remarks, Dr. Nelson states, "... and finally, range grazing will be better integrated with other multiple-uses, so that livestock grazing is both an end product and a management tool on the National Forest System." We hope the oft-repeated Forest Service direction to begin implementing this integrated use nationwide will begin soon and with enthusiastic determination. Only then can livestock grazing and riparian resources coexist in a healthy condition and only then will deteriorated riparian ecosystems recover.

We have been advised of the Forest Service's concern for riparian habitat management and understand your office is currently preparing a supplemental policy statement to give added field guidance on the issue. Several regions have also developed riparian management guidelines most notable of which is the interagency effort in Region 6, where federal and state agencies have finalized field guidelines. Forest Service research stations have published numerous reports and are conducting varied research on grazing and riparian management issues. The Intermountain Forest and Range Experiment Station (Region 4) is one of the leaders in assisting land managers with viable options for fisheries and land management decisions. Research must continue to assist management in developing reasonable and sound alternatives for riparian management. Nevertheless, it is no longer acceptable for range managers and administrators to delay on-the-ground actions to improve deteriorated riparian habitat because of the need for "continued research." We realize the socio-economic and political pressures which must be faced in implementing both grazing and riparian management objectives. But at the same time we believe that land and water resources, once restored, can be maintained in a productive state, able to sustain reasonable land use demands for the support of livestock and fisheries-riparian values.

The American Fisheries Society would welcome the opportunity to meet with you and Dr. Nelson at your convenience to discuss further these concerns about Forest Service Management of livestock grazing and riparian ecosystems. In the meantime, if I can provide further clarification of our views, please give me a call.

Sincerely yours,

Carl Sullivan

Carl R. Sullivan
Executive Director

CRS/lg

CC Dr. Thomas C. Nelson - U.S. Forest Service
Richard H. Stroud - President, AFS
Selected Members - Natural Resource Council of America
Senator John Melcher, Chairman Subcommittee on Environment, Soil Conservation and Forestry
Senator Henry Jackson, Chairman Committee on Interior and Insular Affairs
Congressman James Weaver, Chairman Subcommittee on Forests
Congressman Sidney R. Yates, Chairman Appropriations Subcommittee on Interior
Gus Speth, Chairman Council of Environmental Quality
Leadership - American Fisheries Society

Dr. Behnke:

Thought you might be interested in this.

Danel

Lee Mills
Aug. 79

104310 - 2401585
16 Dec-79

AZ 8021 Zürich
31. Jahrgang / Nr. 9
September 1980

Petri-Heil

Mit farbigem Hechtposter Seite 10

Redaktion Tel. 01 / 251 61 71
Bächtoldstr. 4, 8044 Zürich

Die unabhängige, illustrierte Sportfischerzeitung

Erscheint monatlich
Jahresabonnement Fr. 32.—

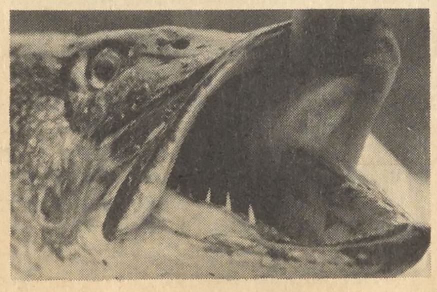
MAURER

SCHWEIZER FABRIKAT

Auch am Volksmodell nun der neue Scharnierdeckel mit Fischmass. Katalog gratis im Fachgeschäft.

Maurer Gümmenen

METALL-VOLKSMODELL



Spieglein, Spieglein an der Wand...

Dieser mächtige Rachen schnappte den Köder eines «Petri-Heil»-Lesers. Wer, wie, wo die kapitalen Fänge dieses Sommers realisierte, erfahren Sie auf Seite 5

Fischereirechtliche Stellungnahme des Eidgenössischen Departements des Innern zu den Kraftwerkprojekten Ilanz

Bundesrat Hürlimann will Fischereigesetz Nachachtung verschaffen!

Bekanntlich haben die Bündner Sportfischer gegen den Entscheid des Regierungsrates des Kantons Graubünden in Sachen Bewilligung für die Kraftwerke Ilanz I und II Verwaltungsgerichtsbeschwerde erhoben. Darin wird verlangt, dass die unbedingt erforderlichen Schutzmassnahmen zugunsten der Fischerei gemäss eidg. Fischereigesetz zugleich mit der Bewilligungserteilung konkret festgelegt werden. Die Bündner Regierung akzeptierte zwar nach unserem Kampf gegen die Kraftwerke, dass das Fischereigesetz auf die Konzession für Ilanz nachträglich anwendbar sei, wollte jedoch die entsprechenden Massnahmen erst nach Abschluss der Kommissionsstudien erlassen. Damit müssten die NOK das Projekt in Unkenntnis der kommenden Auflagen erstellen (z. B. Mindestwassermenge), und aus diesem Grund haben auch die Kraftwerke den regierungsrätlichen Entscheid angegriffen. Sie lehnen die Anwendung des Fischereigesetzes überhaupt ab — allerdings mit sehr schwachen Argumenten. Das Bundesgericht bat das Eidg. Departement des Innern in dieser Sache zu einer Stellungnahme über die Anwendbarkeit des Fischereigesetzes. Das Departement Hürlimann reichte am 10. Juli ein 13seitiges Exposé ein, das wir auszugsweise publizieren:

Die Ilanzer Kraftwerke: Neuanlagen oder bestehende Anlagen?

Die Konzessionserteilung für die Ilanzer Werke erfolgte im Jahre 1964, d. h. unbestrittenermassen *vor* dem Inkrafttreten des FG. Mit der Bauausführung wurde dagegen ebenso eindeutig erst *nach* diesem Zeitpunkt begonnen, nämlich im Jahre 1979. Auch die endgültige Projektierung erfolgte bereits unter der Herrschaft des neuen Rechts.

Die im FG vorgesehene Unterscheidung zwischen Neuanlagen und bestehenden Anlagen lässt nach unserer Auffassung nur diesen Schluss zu: Neuanlagen sind all jene Werke, die im Zeitpunkt des Inkrafttretens des FG noch nicht bestanden; dagegen sind unter Altanlagen Werke zu verstehen, die zu diesem Zeitpunkt entweder schon fertiggestellt oder doch zumindest bereits im Bau waren. Die Kraftwerke Ilanz I und II befanden sich im Zeitpunkt des Inkrafttretens des FG erst im Stadium des generellen Projekts. Die entsprechenden Projekte wurden später (1977) sogar nochmals überarbeitet. Ein generelles Projekt, das erst auf dem Reissbrett besteht, stellt nach der hier vertretenen Auffassung jedenfalls keine «bestehende Anlage» im Sinne des FG dar, weshalb nur die Behandlung als Neuanlage in Frage kommt. Dieses Ergebnis entspricht übrigens auch der ratio legis: Die Unterscheidung zwischen neuen und alten Eingriffen im FG beruht nämlich auf der ohne weiteres einleuchtenden Erkenntnis, dass bei Altanlagen die Sachzwänge in aller Regel kaum mehr völlig befriedigende Massnahmen im Interesse der Fischerei zulassen, wogegen solche Vorkehren bei noch nicht ausgeführten Projekten mit vertretbarem Aufwand vorgesehen werden können.

Zum selben Ergebnis gelangt man übrigens auch aufgrund der allgemeinen Regeln über das intertemporale Recht. (...). Aufgrund dieser Ueberlegungen gelangen wir mit der Vorinstanz zum Schluss, dass die Kraftwerke Ilanz I und II grundsätzlich als Neuanlagen im Sinne des Art. 24 FG zu behandeln sind und folglich nur mit der besonderen fischereirechtlichen Bewilligung gebaut werden dürfen.

Wurde das FG richtig angewendet?

Der Auffassung der Vorinstanz vermögen wir nicht zu folgen. Mit den beiden

Lesen Sie bitte weiter auf Seite 3

Diesen Monat

Schweizer Sportfischer-Brevet

Jetzt ist es Zeit, sich auf das Brevet vorzubereiten. Wir informieren Sie über diese freiwillige Weiterbildungsmöglichkeit auf Seite 3 und 4

5 Tage Antistress

offerieren wir unseren Lesern am Lungernsee zum günstigen «Alles inbegriffen»-Preis von Fr. 295.— auf Seite 8

Schnapsprobleme

Wer Wasser aus dem Zugersee trinkt, sollte nicht mehr autofahren! Warum verraten wir in unserer Anklage auf Seite 12

Aktuell

Ueber das sommerliche Geschehen am Fischwasser informieren wir Sie auf Seite 14 und 15

Wein, Weib und . . . Fische

Diese Worte charakterisieren unsere (kulinarische) Rubrik «Wir Fischerfrauen» auf Seite 17 und 19

Auf ein Wort

Es harzt bei der Behandlung des Umweltschutzgesetzes, das seit Monaten schon vor einer nationalrätlichen Kommission liegt: Ende August traf sich das parlamentarische Gremium zur fünften mehrtägigen Sitzung (eine erste Tagung wurde bereits im Februar dieses Jahres durchgeführt). Trotzdem ist man erst bei Artikel 9 des 57 Artikel umfassenden Gesetzesentwurfes angelangt. Da nicht anzunehmen ist, das Beratungstempo werde sich erhöhen, wird die Vorlage kaum vor der Sommersession 1981 für das Plenum spruchreif.

Allerdings muss man für den schleppenden Gang der Beratungen ein gewisses Verständnis aufbringen: Die zur Diskussion stehende Materie ist tatsächlich «komplex», wie sich Kommissionspräsident Schmid (soz., SG) ausdrückte.

Es harzt

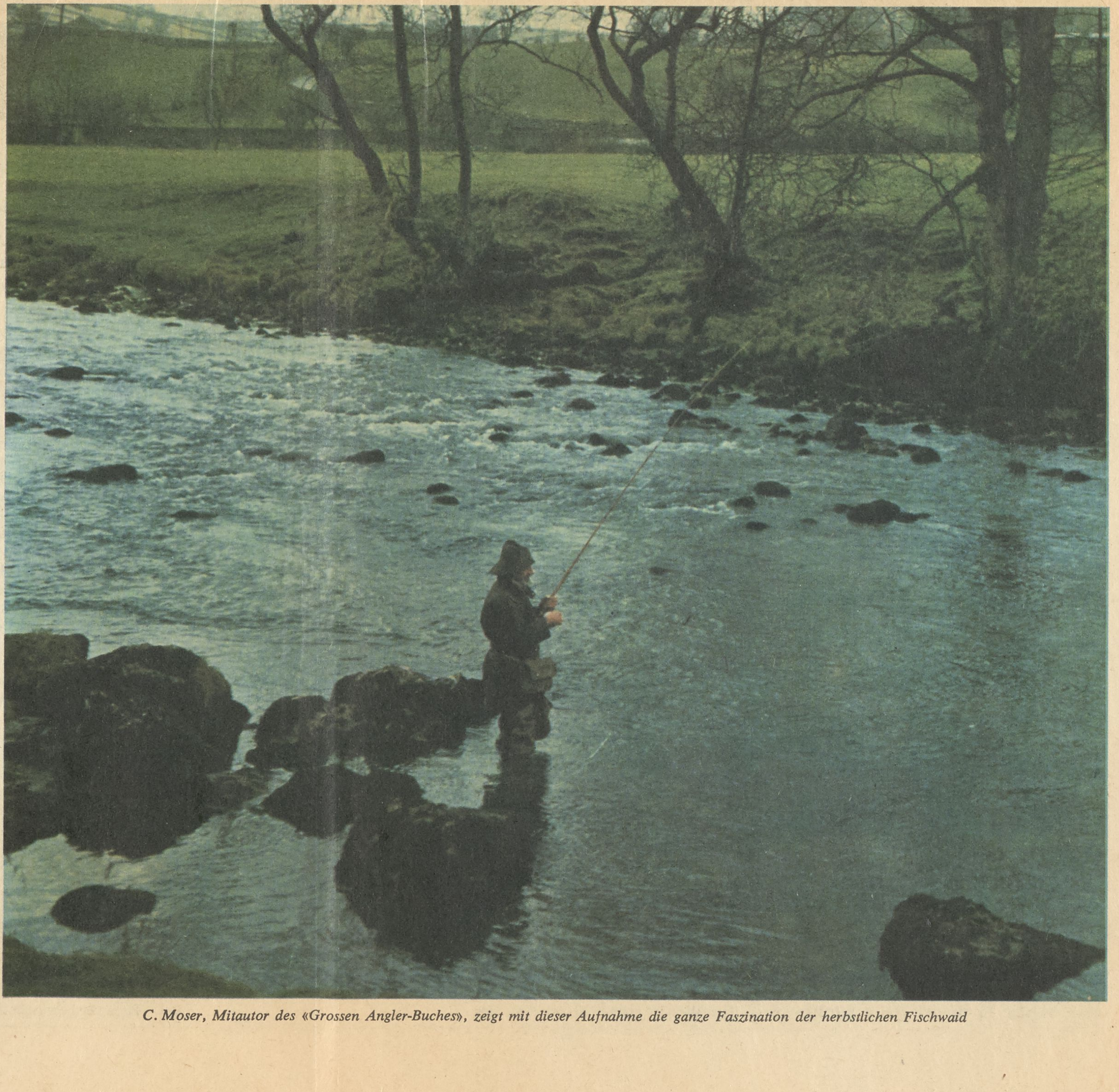
Und man befindet sich gewissermassen auch auf «Neuland», wenn man von den gesetzgeberischen Erfahrungen im Bereich des Gewässerschutzes absieht. Die Kommissionäre nehmen ihre Aufgabe denn auch entsprechend ernst: Zusätzlich zur umfangreichen bundesrätlichen Botschaft ist sie bestrebt, sich aus erster Hand zu informieren. Sie führt deshalb Hearings mit Experten und Besichtigungen an der «Front» durch. Ein solches Programm ist aber zeitraubend.

Positiv auch der manifeste Wille zum Konsens und zur Zusammenarbeit im Schosse der Kommission. Man will offenbar (endlich!) den in der Verfassung verankerten Umweltschutzgedanken und -auftrag verwirklichen, nicht blindlings zwar, sondern wohlbedacht-pragmatisch. Da dieser Pragmatismus, diese Ausrichtung auf das technisch Mögliche und wirtschaftlich Verantwortbare den ganzen Gesetzesentwurf auszeichnet, erstaunt es weiter nicht, dass die Kommission früher schon einstimmig für Eintreten plädiert und die ersten neun Artikel mit bloss geringfügigen Abänderungen verabschiedet hat.

Unter diesen ersten Artikeln, die die grundsätzlichen Aspekte des Umweltschutzes (präziser: des Immissionsschutzes) regeln, befindet sich auch jener, der die sog. Umwelt-Verträglichkeitsprüfung verankern soll: Künftig sollen alle Grossanlagen, die die Umwelt erheblich belasten können, in bezug auf ihre Nebenwirkungen genau überprüft werden. Von dieser Prüfung, die man bisher einzig in den USA kennt, werden Anlagen wie z. B. Hochleistungsstrassen, Bahnanlagen, Flugplätze, Industrieanlagen, Waffen- und Schiessplätze, Deponien, Kraftwerke usw. betroffen. Interessanterweise wurde gegen das Prinzip nicht grundsätzlich opponiert. Fraglich ist allerdings, ob es bei der Behandlung von Artikel 49 des Umweltschutzgesetzes ebenso klaglos gehen wird: Dort wird nämlich den gesamtschweizerischen Umweltschutzorganisationen ein Beschwerderecht eingeräumt, ein Vorhaben, das namentlich in Wirtschaftskreisen nicht ohne weiteres goutiert wird. Die diesbezügliche Ausmarchung steht allerdings erst noch bevor. *HUB*

Die vielseitige herbstliche Fischwaid

Noch stellen wir den Forellen nach, aber bald werden sie in Ruhe ihre Hochzeit vorbereiten können. Jetzt wird die Aeschenfischerei aktuell (Seite 6), aber auch Zander und Hecht (Seite 7 und 10) können ein Fischerherz erfreuen. Die starke Anziehungskraft des Angelns geht aber nicht vom Bedürfnis nach reicher Beute aus, sondern vielmehr von der Erkenntnis, dass dieser schöne Sport uns wieder Naturverbundenheit, Entspannung und wahre Erholung zu bieten vermag. Ein Standardwerk der Sportfischerei vermittelt uns das notwendige Basiswissen auf Seite 11



C. Moser, Mitautor des «Grossen Angler-Buches», zeigt mit dieser Aufnahme die ganze Faszination der herbstlichen Fischwaid

[1980]

Pro + Contra (Diskussionsforum)

Leserbriefe sind uns jederzeit willkommen. Bevorzugt werden kurzgefasste Zuschriften, die sich auf die aktuellsten Artikel des «Petri-Heil» beziehen. Für den Inhalt der veröffentlichten Zuschriften trägt die Redaktion keine Verantwortung.

[A Record Catch]

Rekordfänge?

Die Hechtfänge des Jörg Nötzli und die darob entflammte Diskussion gehören der Vergangenheit an. Sie waren für jene Fischerfreunde nützlich, die nächstens das Glück haben, selbst einen Rekordfisch zu fangen.

Wir Fischer wissen um unsere Neider. Wir wissen aber ebensogut, dass wir, was Anzahl Fische, Fangmasse oder -gewichte anbelangt, von unseren fischenden und nichtfischenden Kameraden nicht immer für ganz voll genommen werden. Wie sonst käme es, dass über vielen Stammtischen heimeliger Fischerbeizlis der sinnige Spruch prangt: «Für Fischer, Jäger und andere Lügner»?

Und deshalb ist mir beim Lesen der erwähnten Episteln aufgerochen, weshalb da verschiedene Zeugen und Angaben gefehlt haben sollen.

Dies, weil ein Kollege von mir, der Oize (kommt vom Oesterreichischen), vermutlich allein aus dem Unterbewusstsein heraus seinerzeit genau das Richtige gemacht hat, was scheinbar notwendig ist, einen Rekordfisch vor sämtlichen zuständigen Jurys und Gremien bestehen zu lassen, und was sich wie folgt zugetragen hat:

> Oize angelte in den Ferien zusammen mit zwei Vereinskameraden hinter der Tariche auf Doubsforellen. Eines Morgens im Mai just fünf Uhr früh fing Oize seine Traumforelle, eine siebenundsechzig Zentimeter lange und dreieinhalb Kilogramm schwere Doubsforelle. Sofort wurden die beiden Kameraden Ugo und Billy ins Bild gesetzt, und ab ging's ins dortige Beizli, wo der Fisch vom Wirtepaar und sämtlichen inzwischen wach gewordenen Gästen bestaunt und begossen wurde.

Ich als Daheimgebliebener erhielt bereits um halb acht Uhr telefonische Kunde von diesem seltenen Fang. Den Rest der Ferien verbrachte die Forelle im Hältertrog des Wirtes, wo sie von einem grossen Publikum während Tagen gebührend bestaunt werden konnte.

Wie ein Lauffeuer verbreitete sich in unserem Dorf, dass Oize mit seinem Fisch heimgekehrt sei und im Stöckli hocke. Eine wahre Völkerwanderung aller Fischereiinteressierten setzte daraufhin ein.

Hier nun sass Oize in seiner Fischerkluft, etwas müde und übernächtigt, mit leicht geröteten, wässrigen Augen bei einem grossen Rugeli — am Boden nebenan besagter Beutefisch. Huldvoll nahm Oize die ihm dargebrachten Ovationen entgegen.

Die Forelle von Oize wurde von mindestens hundert Fischern und ebenso vielen Nichtfischern gesehen. Er ist seitdem mit und ohne Fisch in allen unseren Fotoalben verewigt, und da hängt er nun fachgerecht präpariert in seiner ganzen Pracht in unserem Stammlokal — der Fisch natürlich, nicht der Oize!

Bastian Rauh

Wie informiert sich ein Sportfischer?

Eine gute Frage. Ich möchte versuchen, eine gute Antwort zu finden. In der Schweiz kennen wir etwa 200 000 Sportfischer. Davon sind 25 % in Vereinen und Verbänden organisiert. Unsere beiden Sportfischer-Zeitschriften erreichen zusammen eine Auflage von knapp 18 000 Stück. Somit ist erwiesen, dass sich bei uns nur *jeder elfte Fischer eine Zeitschrift leistet.* Natürlich gibt es bessere Möglichkeiten, sich über Aktualitäten zu informieren. Landauf und landab hat es in jeder Beiz einen runden Tisch. Hier holt sich der zünftige Petri-Jünger seine News und Tips. Dass dabei einige Sachen nicht ganz den Tatsachen entsprechen, ist ja weiter nicht schlimm . . .

Es gibt ja höhere Verbandsfunktionäre, die auch keine Zeitung über die Fischerei abonniert haben. Kürzlich meinte ein solcher wörtlich: «Ich sehe keinen Grund, eine Sportfischerzeitung zu abonnieren, beinahe dasselbe steht auch in den Tageszeitungen.» Bei den gleichen Leuten fragt man sich, woher das enorme Fachwissen und die manchmal etwas kuriosen Ideen kommen.

Vielfach hört man als Ausrede, eine solche Zeitschrift ist zu teuer oder es hat zuwenig Beiträge, die interessieren. Wer sich aber täglich eine Boulevardzeitung kauft, gibt im Jahr an die 200 Franken aus. Wenn sich aber die Sportfischer entschliessen könnten, unsere Fachblätter zu beschaffen, hätten die Verlage viel mehr Geld zur Verfügung. Damit könnten mehr Artikel gekauft und die Zeitung noch umfangreicher gestaltet werden. Zu wünschen wäre, dass mindestens jeder organisierte Fischer eine Sportfischerzeitung abonniert. Meine Idee wäre: Jeder Abonnent bringt einen neuen, und die Auflage ist auf einen Schlag verdoppelt.

A. Schweizer

Intermediate-Fliegenschnüre (Nonsensplusultra)

Zum Artikel der «neuen» Fliegenschnüre von MCC in der «Petri-Heil»-Ausgabe vom August 1980 möchte ich folgendes sagen:

Die Industrie ist heute in der Lage, Fliegenschnüre anzubieten, die auch in unseren leider nicht mehr ganz sauberen, phosphathaltigen Gewässern gut schwimmen. Entwickelt wurden diese Schnüre, weil nur eine *schwimmende* Schnur optimales Trockenfliegen- und zum Teil Nymphenfischen erlaubt. Mit dieser Meinung befinde ich mich übrigens in guter Gesellschaft, denn auch Leute wie Charles Ritz, Frank Sawyer, Oliver Kite usw. haben diese Tatsache immer wieder demonstriert und in ihren Publikationen festgehalten. Tausende von Fliegenfischern sind zudem heute glücklich, dass es schwimmende Schnüre gibt, nur einer nicht, für ihn ist die leicht sinkende Schnur das Optimum.

Lieber Herr MCC, ich schätze den Individualismus; was ich aber nicht so schätze ist, wenn einer nun hingeht und eine persönliche Vorliebe in einem Artikel als allgemein gültig erklären will, dabei aber zu unrichtigen Beweismitteln greift.

So ist zum Beispiel unhaltbar, dass das Wasser an einer versunkenen Schnur weniger «zieht» als an einer, die auf dem Oberflächenfilm schwimmt. Ich möchte auch ganz gerne wissen, wie Sie mit einer versunkenen Schnur beim Nymphenfischen feine und feinste Bisse bemerken wollen. Es ist zwar richtig, dass bei klarem Wasser eine Schwimmschnur bei Sonnenschein auf dem Gewässerboden ihren Schatten hat; aber auch eine Intermediate-Schnur hat ihren Schatten. Zudem empfehle ich Ihnen bei einer solchen Situation, statt die Fliege direkt an der Fliegenschnur anzubinden, es einmal mit einem überlangen Vorfach mit feinster Spitze zu versuchen (auch das feinste Vorfach ist zwar nicht schattenlos und wird vom Fisch zudem mit grösster Wahrscheinlichkeit zwar gesehen, jedoch nicht als störend «eingestuft»).

Theoretisch ist es auch richtig, dass mit einer relativ dünnen und schweren Fliegenschnur wegen des geringeren Luftwiderstands weiter geworfen werden kann. Sie sprechen in Ihrem Artikel jedoch von fischereilichen Vorteilen der Intermediate-Schnüre, und nicht vom Casting-Sport.

Und auch hier erlaube ich mir zu fragen, wie Sie einen Fisch, der Ihre Trockenfliege nimmt, «anschlagen» wollen, wenn zwischen Fliege und Rute zwanzig Meter versunkener Schnur liegen? Auch beim klassischen «up stream»-Nymphenfischen wünsche ich Ihnen mit einer Intermediate-Schnur viel Glück.

Nach meinen eigenen Versuchen musste ich zum Schluss gelangen, dass Sie offenbar für sich selbst das Fischen mit der «dreggenden» Trockenfliege erfunden haben. Diese Art der Fischerei, die beim Einnachten mit Sedges betrieben sehr erfolgreich sein kann, ist erstens schon recht alt und bekannt und kann zweitens mit einer Trockenschnur genausogut ausgeführt werden.

Sicher kann man, in flachen Gewässern zumindest, mit der Intermediate-Schnur mit dem Streamer fischen, es geht in solchen Gewässern aber auch mit der Trockenschnur. Sind die Gewässer tiefer, ich selbst fische zum Beispiel sehr gern und oft mit dem Streamer im Linthkanal, dann kommt man ohne eine sinkende oder schnell sinkende Schnur (evtl. Schusskopf) einfach nicht aus, wenn man den Streamer dorthin bringen will, wo die Grossen sind, nämlich ins Mittelwasser oder knapp über den Grund.

In einem Punkt muss ich Ihnen, Herr MCC, uneingeschränkt Recht geben. Keine Trockenschnur — und man kann sie reinigen und pflegen wie man will — schwimmt ewig. Winzige Bruchstellen sorgen mit der Zeit dafür, dass jeder seine Intermediate-Schnur bekommt. Für die meisten Trockenfliegenfischer ist dann jedoch der Moment gekommen, wo sie zum Fischereiartikelhändler gehen — und Sie werden es kaum glauben —, um sich eine neue Fliegenschnur der Klasse F (wie floating) zu kaufen.

Mit freundlichen Grüssen *Heinz Ryffel*

«Fischgewässer und ihre Bewirtschaftung»

Einzelanmeldungen für diese Vortragsreihe von M. Straub an der ETH Zürich (siehe Inserat Seite 13) nimmt die Redaktion «Petri-Heil» entgegen: Telefon 01 / 251 61 71.

Fast keine Brevetierung! Oder ein modernes Märchen . . .

Mein Mann macht gelegentlich für die Sportfischerzeitung «Petri-Heil» Filmvorführungen für Interessierte und Gleichgesinnte, im allgemeinen Sportfischer genannt. Ausserdem sind in letzter Zeit Brevetierungen, zu deutsch Fischerprüfungen, sehr gefragt, und ein Filmvortrag lockert die Atmosphäre. Da er dies normalerweise nur in der näheren Umgebung und alleine tut, sagte mir Büren an der Aare nicht allzuviel.

Ganz kurzfristig kam er dann auf die Idee, ich solle ihn begleiten, ausnahmsweise einmal, damit die Fahrt nicht so langweilig sei. Schliesslich stellte sich heraus, dies sei in der Nähe von Biel — also nicht gerade auf dem Weg vom Zürcher Oberland. Also liess ich mich überreden. Wir wählten das schnellere und radiobestückte unserer beiden Autos und waren pünktlich am Treffpunkt in Zürich, um die gesamte Ausrüstung inklusive Brevetierungskram in Empfang zu nehmen. Wir hatten noch gut zwei Stunden Zeit bis zu unserem Ziel. Trotz Feierabendverkehr kamen wir gut voran, als mein Liebster die Stampfenbachstrasse hinab ganz fürchterlich zu fluchen begann. Es dauerte einige Schaltsekunden, bis ich begriff, dass die Bremsen nicht mehr wollten und dies ausschliesslich meine Schuld sei. Zum Glück funktionierte die Handbremse, und in aller Eile suchten wir einen Parkplatz, und wir fanden sogar einen! Was machen? Auf zum nächsten Telefon . . . Es ist zu kompliziert zu erzählen, wen wir alles anriefen. Vom zuständigen Redaktor bis zum besten Kollegen, es war Freitagabend und niemand zu Hause. Um wenigstens die Brevetierung zu retten, beschlossen wir, mit einem Taxi ins heimatliche Uster zurückzufahren und dann mit dem anderen Wagen nach Büren. Ich versuchte mit aller Vorsicht klarzumachen, dass dies höchstens mit zweistündiger Verspätung und einigem Risiko zu schaffen sei, aber ich glaube nicht, dass auch nur ein vernünftiges Wort aufgenommen wurde. Da weit und breit kein Taxistand zu sein schien, postierten wir uns gut sichtbar am Strassenrand und «harrten» der Dinge. So mindestens zehn bis fünfzehn Taxis brausten vorbei, natürlich besetzt. Plötzlich, vollkommen unverständlich, bleibt vor unserer Nase ein Auto stehen — «Hoi Gusti, was machst Du denn da!» Wer ist eigentlich der Gott der Fischer und hat ein verzweifeltes Stossgebet meines Gatten aufgefangen? Ein Fischerkollege steigt aus. Für meine Begriffe geht alles viel zu schnell, es wird umgeladen, ich weigere mich mitzufahren, mein Mann ist unterwegs nach Büren an der Aare! Ich stehe da mit Kollege und Frau, wir retten uns ins nächste Café.

Nach einer gewaltigen Verschnaufpause wird mir erst richtig bewusst, was da wirklich passiert ist und dass es in der heutigen egozentrischen Welt wahrhaftig noch gute Kollegen gibt . . . Die beiden gehen friedlich nach Hause, und ich reise per SBB nach Uster. Nach telefonischer Verständigung stelle ich fest, dass mein Mann tatsächlich mit geringfügiger Verspätung am Bestimmungsort eingetroffen ist — der Brevetierungsabend ist gerettet. Zu mitternächtlicher Stunde bin ich wieder nach Zürich unterwegs, um meinen Mann abzuholen. Nach dem x-ten Umladen der Gerätschaft liefern wir auch diese wieder ab, bringen unser «Mietauto» zurück und landen ziemlich spät — oder früh — und erschöpft zu Hause.

Wenn das kein modernes Märchen ist?

hej.

Wie kann der Ertrag eines Gewässers gesteigert werden?

Von Werner Fahrni

Die Erträge unserer Fischgewässer werden von zahlreichen Gegebenheiten beeinflusst. Zu den wichtigsten Voraussetzungen für einen bestmöglichen Fischbestand gehören Gewässerpflege, dauernd genügende Mindestwassermengen, Ausschaltung von Verschmutzungsquellen, durchdachte Fischereiverordnung usw. Daneben gibt es Verbesserungsmöglichkeiten, denen weniger Beachtung geschenkt wird, die wir aber einmal etwas näher unter die Lupe nehmen möchten.

Da wäre die Sorgfalt beim Jungfischeinsatz zu erwähnen. Die Art und Weise, wie der Fischeinsatz vorgenommen wird, kann ebenso grosse Auswirkungen auf das Resultat haben wie die Anzahl eingesetzter Fische. Jeder Einsatz von Brütlingen, Sömmerlingen oder Jährlingen bedeutet nicht nur irgend ein Entleeren einer Tonne oder eines Kübels irgendwo am Wasser. Besondere Beachtung ist bereits dem Transport der Jungfische zu widmen und jeder Temperaturunterschied von einem Wasser zum anderen ist zu vermeiden. Dazu gehört ein Thermometer. Meistens ist es unerlässlich, aus dem Einsatzgewässer steigende Wassermengen in die Transportmittel einzufüllen bis der Ausgleich erreicht ist. Ein brüsker Temperaturwechsel kann für die Jungfische katastrophale Folgen zeitigen, ohne dass man sofort etwas bemerkt. Es lohnt sich deshalb für diese Arbeit genügend Zeit zu reservieren.

Beim Einsatz ist auf eine gute Verteilung zu achten. In Fliessgewässern werden die Jungfische in kleine Läufe in der Nähe von Gräsern oder Aesten eingesetzt, die ihnen Schutz und Unterschlupf bieten während der Akklimatisation. Man vermeide den Einsatz in der Nähe von Standorten grosser Forellen.

Wo die Fischereivereine mit den für den Fischeinsatz zuständigen Kantonsinstanzen zusammenarbeiten, sollte man auf eine Equipe von Vertrauensmänner zählen können, die über die erforderlichen Kenntnisse und Erfahrungen auf diesem Gebiet verfügt. Dies gewährleistet ein bestmögliches Resultat und vermeidet unnötige Verluste.

Heutzutage wird der Fischtransport durch den Einsatz von Sauerstoffgeräten erleichtert. Trotzdem sollte die Transportzeit auf ein Minimum beschränkt werden, insbesondere bei warmen Temperaturen sollte jeder unnötige Aufenthalt weggelassen werden. Wissenschaftliche Untersuchungen haben gezeigt, dass die Vibrationen während des Transportes die Fische stark ermüden. Jeder, der mit dem Fischeinsatz zu tun hat, sollte deshalb seine Aufgabe zuverlässig und speditiv erfüllen, bevor er sich im nächsten Gasthaus davon erholt. Nach getaner Arbeit ist aber ein Glas als Belohnung bestimmt angebracht.

Ein nicht zu vernachlässigender Faktor ist die Beschaffung des Besatzmaterials. Wenn immer möglich sollte es aus der gleichen Region oder zumindest aus gleichartigen Gewässern in derselben Höhenlage stammen.

Aber auch das Verhalten der Sportfischer beeinflusst den Fischbestand und -ertrag. Bestimmt haben Sie in stark befischten Bächen schon tote Forellen auf dem Grund gesehen. Die meisten davon sind untermässig. Die bedauerliche Sterblichkeit ist leider zu oft das Resultat unsportlicher Behandlung durch die Angler. Ja, ich weiss, dass jedem von uns passieren kann, einen Fisch zurückzusetzen, der nicht überleben kann. Aber es gibt noch zuviele Sportfischer, die dem untermässigen Fisch zuwenig Respekt entgegenbringen. Zuviele quälen einen Fisch, nur um keinen Haken zu verlieren. Auf diesem Gebiet wird mehr gesündigt, als man annimmt und deshalb bringen Aufklärung und Kontrolle nicht zu verachtende Resultate.

Wenn ein Fisch den Köder geschluckt hat, die Hakenspitze im Maul nicht mehr sichtbar ist, sondern im Hals sitzt, darf man sich über die Ueberlebenschance des Fisches keine Illusionen machen, wenn man versucht den Haken herauszubringen. Man gibt dem Fisch eine bedeutend grössere Chance, indem man das Vorfach sofort abschneidet und sorgfältig darauf achtet, keinerlei Zug auf die Schnur auszuüben. Wer seine Beute lebend transportiert, hat bestimmt einschlägige Erfahrungen gemacht.

Es liegt in unserem Interesse, Verluste durch unsachgemässe Behandlung von untermässigen Fischen einzuschränken. Ein grosser Fortschritt wird erreicht, wenn dem Fischer klar wird, dass jede Jungforelle bedeutend mehr Wert hat als ein noch so teurer Haken.

Auch untermässige Fische, die ohne Verletzungsgefahr vom Haken befreit werden können, sollten mit grösster Sorgfalt behandelt werden: Die Hände vor jeder Berührung nass machen oder noch besser das Hakenlösen im Wasser vornehmen, nie drücken mit den Fingern, vorsichtig zurücksetzen und nie werfen. Achtung, Aeschen sind noch heikler als Forellen!

Jeder richtige Sportfischer empfindet Freude, wenn der Fisch nach vorsichtiger Behandlung munter im Lauf oder in der Tiefe verschwindet. Im Gegenteil wird Enttäuschung und Unmut aufkommen, wenn ein Untermässiger den Köder geschluckt hat.

Und gerade dagegen können wir auch Vorbeugungsmassnahmen treffen. Wer mit dem natürlichen Köder fischt, muss konzentriert bleiben und seine Leine stets beobachten. Wenn man ohne Zapfen fischt, versieht man die Schnur mit einer oder zwei farbigen Markierungen. Beim geringsten Anzeichen, schlägt man ohne zu übertreiben an. Die Sicht spielt dabei eine grosse Rolle, denn das Auge kann den Anbiss wahrnehmen, bevor man ihn spürt. Je kleiner der Köder, um so schneller muss der Anschlag erfolgen.

Bei den künstlichen Ködern besteht wenig Gefahr, dass sie geschluckt werden. Mit der Trockenfliege kommt ein Schlukken praktisch nicht vor. In den meisten Fällen spürt der Fisch augenblicklich, dass er getäuscht wurde und versucht den Köder sofort auszuspucken oder loszuwerden. Somit wird er meistens an den Lippen, hie und da in der Zunge gehakt. Jedenfalls bleibt der Haken sichtbar und kann ohne grosse Mühe entfernt werden.

Ohne Zweifel werden kleine, natürliche Köder am meisten geschluckt: Maden, Bienenmaden, Larven, kleine Würmer usw. Mit der Verwendung eines Zapfens kann das Risiko etwas gemildert werden, aber nicht in allen Gewässern ist die Zapfenfischerei angebracht.

Wir wissen, dass die Hakengrösse im Verhältnis zum verwendeten Köder und zum gewünschten Fisch gewählt werden muss. Man begreift auch leicht, je kleiner der Haken, desto schneller wird er geschluckt. Da wir stets aus zwei bis drei Grössen wählen können, entscheiden wir uns immer für den grösstmöglichen. Zum Beispiel Nr. 8 bis 10 für die Made auf Forellen, also Nr. 8 oder sogar Nr. 7 wenn die Maden gross genug sind.

Es ist also in einem gewissen Ausmass möglich, das Schlucken und damit Verluste von Fischen zu verhindern. In dieser Beziehung sollte sich der erfahrene Fischer gegenüber dem Anfänger auszeichnen. Allerdings kommen Momente oder Tage, während denen die Besten unter uns einen Unfall nicht vermeiden können. Besonders wenn die Forelle hungrig ist. Doch meistens sind es dann in erster Linie die Kleinen, die sich auf unsere Köder stürzen und so tun wir besser daran, uns für eine Weile ans Ufer zu setzen um auszuruhen oder die Natur zu beobachten. Wenn wir nach einer Weile wieder in Aktion treten, sind wir ruhiger und konzentrierter. Zudem sind Beobachtungen am Wasser nie verlorene Zeit!

«Petri-Heil»-Gewässerschutzfonds

August 1980

Kassastand 1. August 1980	Fr. 3489.05
Eingänge August:	
W. M. in Z.	Fr. 15.—
A. Sch. in St.	Fr. 25.—
H. K. in Z.	Fr. 10.—
Kassastand 31. August 1980	Fr. 3539.05

Petri-Heil

Chefredaktion
Hans U. Büschi, Hansjörg Dietiker (Vorsitz), Kurt Lienhard, Heinz Renz, Jules Rindlisbacher.

Ständige Mitarbeiter
Theo Camenzind, Mario C. Chiari, Pierre Düby, Werner Fahrni, Beppi Franchi, Dorothe Freiburghaus, Bruno Frick, Hermann Fritzsche, Roland Furrer, Heinz Kohlbekker, Hansruedi Küttel, Meinrad Lingg, Walo Luginbühl, Ernst Mühlheim, Kurt Müller, Dr. Ernst Rohrer, Prof. Heinz Schurig, Alex Schwab, Markus Vetsch, Hans-Ruedi Wäckerli.

Verlag und Inseratenverwaltung
Graf + Neuhaus AG, Bächtoldstr. 4, 8044 Zürich, Tel. 01 / 251 61 71, PC 80-45170
Jahresabonnement Fr. 32.—, Preis der einspaltigen Millimeterzeile 69 Rp.

Rotationsdruck
Offset + Buchdruck AG, Zürich

Redaktions- und Inseratenschluss
Am 1. des Monats

Sportfischerdienste
«Petri-Heil»-Bilderdienst, -Filmdienst, -Gewässerschutzdienst, -Touristikdienst, -Vereinsdienst: Bächtoldstr. 4, 8044 Zürich

Warum?

sind die Speer-Boote innert kürzester Zeit
eines der beliebtesten Sportfischerboote geworden?

Weil sie sehr stabil sind (Doppelschalenbau)

Weil sie sehr robust in bester Schweizer Qualität gebaut sind

Weil sie äusserst geräumig sind, viel Platz in der Kabine und im Cockpit viele Staufächer haben, grosser Fischkasten

Weil sie kurze Lieferfristen haben

Weil sie ...
Kommen Sie und sehen Sie sich die Speer-Boote an, Sie werden noch mehr Vorzüge finden!

SPEER 600
SPEER 550

Speer 600
Länge 6 m, Breite 1,85 m
Gewicht etwa 450 kg, Tiefgang 0,15 m

Speer 550
Länge 5,50 m, Breite 1,60 m
Gewicht etwa 300 kg, Tiefgang 0,15 m

Jetzt besonders günstig! Herbstrabatt!

Bau + Verkauf:
Bootswerft Thoma, 8872 Weesen Telefon 058 / 43 14 45

Wegen Todesfall
günstig
zu verkaufen

1 Fischerboot

Holz, Johnson-Motor, 9 PS, komplette **Schleppeinrichtung,** Brente, Feumer

Tel. 061 / 47 19 13
od. 037 / 63 24 97

VFGS

Das VFGS-Signet am Fischereiartikelgeschäft gibt Ihnen die Gewissheit, dass hier hinter dem gebotenen Sortiment grosse Erfahrung, prompter Service und eine zuverlässige Beratung stehen.

VFGS

FIBATUBE LTD.

Die Fibatube Ltd. ist Herstellerin der berühmten Blanks aus Kohlefaser und Hohlglas für die Firma Hardy.

Fibatube-Blanks zeichnen sich durch eine exakte Verarbeitung, aber auch durch eine hervorragende, rasche Aktion im Verhältnis zum leichten Gewicht aus.

Diesen Monat aktuell:

Bauen Sie sich Ihre Aeschenrute selbst!

Wir Fibatube-Händler bieten Ihnen die Blanks für die Matchmaker-Ruten (siehe Hardy-Inserat) in fertiger, dreiteiliger Ausführung an.
Wir beraten Sie gerne!

Matchmaker Blanks

12'	365 cm	Fr. 79.—
13'	396 cm	Fr. 95.—
14'	427 cm	Fr. 110.—

Die unten genannten Fachhändler bieten Ihnen auch eine gute Auswahl an Zubehörteilen für den Rutenbau an. Sie beraten Sie gerne mit viel Fachwissen und geben Ihnen selbstverständlich auch eine exakte Bauanleitung mit.

Fibatube-Blanks sind erhältlich bei:

Jakob Weber, Winterthur	**052 / 22 10 69**
Fischerei + Sportartikel AG, Zürich	**01 / 211 55 40**
A. + H. Hebeisen, Zürich	**01 / 301 22 21**
Eugen Kern, Dübendorf	**01 / 821 52 49**

Generalvertretung für die Schweiz:
A. + H. Hebeisen
Schaffhauserstr. 514, 8052 Zürich

FIBATUBE LTD.

Wo man sich trifft

Adliswil:	Fliegenfischerzunft Jeden letzten Mittwoch im Monat ab 19 Uhr im Restaurant Kantine, Allmend/Zürich.
Altenrhein:	Restaurant zum Schiff (SFV Altenrhein).
Bern:	Angelfischerverein Bern, jeden Freitagabend Rest. National, Bern SFV Bern, jeden Freitag ab 19.30 Uhr Hotel Metropol, Bern
Bremgarten:	Fischer-Club Bremgarten, Stammlokal Hotel Adler, Ruhetag: Sonntag
Champfèr:	Hotel Primula, Champfèr, im Zentrum des Oberengadiner Fischerparadieses.
Chur:	Gasthaus Gansplatz (Casting-Club Chur, jeden Dienstagabend, Fischereiverein Chur, jeden Mittwochabend).
Einsiedeln:	Nach dem Sihlsee- oder Bachfischen zum Fischerlatein ins Rest. Schwyzerhüsli
Gersau:	Seehotel Schwert bekannteste Fischküche der Schweiz, täglich frische Fische. Tel. 041 / 84 11 34.
Grabs:	Hotel Kurhaus Voralp. Tel. 085 / 6 22 71.
Haag:	Hotel Kreuz, Aufenthaltsort der Sportfischer im St. Galler Rheintal.
Meilen:	Hotel Löwen (SFV Meilen, jeden letzten Freitag im Monat ab 20 Uhr).
Rümlang:	Rest. Bahnhof, Marcel Zeller, Stamm, Fischküche.
Walenstadt:	Restaurant Löwen (SFV Walensee, jeden ersten Samstag im Monat ab 20 Uhr).
Zollikofen:	Rest. Schloss Reichenbach, Fam. A. Schneider-Iseli, 3052 Zollikofen, Tel. 031 / 57 00 20, Stammlokal der Jünger Petri.
Zürich:	Restaurant Vorderer Sternen am Bellevue: Stamm des Seesportfischervereins der Stadt Zürich jeden Sonntag von 10 bis 12 Uhr sowie jeden Freitagabend im Fischerstübli, Bootsplatz Tiefenbrunnen von 17 bis 22 Uhr.

Sportfischer-Stammlokal

Dienstag bis Freitag
7.30 bis 11.45 und
13.30 bis 18.30 Uhr

Samstag durchgehend
7.30 bis 16 Uhr
Montag geschlossen

«Findsch Aeschefische au en Hit,
nimm immer Romi's Ruete mit»

Für die Aeschensaison:

Romi's Spezialruten

nach Ihren Wünschen angefertigt (bitte frühzeitig bestellen)

Eine weitere Spezialität sind unsere handgefertigten Fischplastiken in Kupfer und Aluminium

Grosse Auswahl an Markenruten und -rollen
Service und Reparaturen in eigener Werkstatt

Fischköpfe präparieren
Versand in die ganze Schweiz
Tageskarten für Limmatreviere

Romi's Fischershop
Molkenstr. 20 (beim Helvetiaplatz)
Telefon 01 / 241 15 25 🅿
8004 Zürich

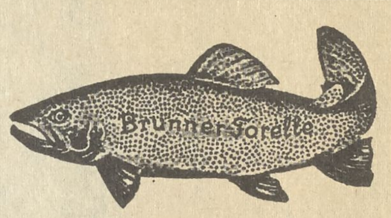
FISH HAWK BRAND

Fliegebinde-Materialien und Werkzeuge usw.

Erhältlich in Angel-Fachgeschäften

E. VENIARD Ltd.
138 Northwood Road
GB-Thornton Heath, Surrey
England, CR4 8Y6
Kein Detailhandel
Grosshandels-Preisliste auf Anfrage

Wer nicht inseriert, wird vergessen!



Wir bieten Ihnen aus unserer eigenen Aufzucht an:

Bachforellensömmerlinge 6—9 cm
Bachforellensömmerlinge 9—12 cm

Lieferbar: ab etwa 1. Oktober 1980

Für Bachforellenjährlinge verlangen Sie bitte eine spezielle Offerte.

Forellenzucht Brunnen, 6440 Brunnen
Telefon 043 / 31 16 80

Forellenfischen in Stetten (Aargau)

Fünf Weiher und ein Bach (150 m) inmitten idyllischer Wiesen und Wald (etwa 1 ha) stehen bei der Alten Mühle in Stetten (Nähe Gnadental an der Reuss) dem Fischer offen. Guter Regenbogenforellen-Besatz (bis 35 cm), Hütte, Grill usw.

Tageskarten (ausgenommen Montag) gratis, gefangene Fische Fr. 15.— pro kg.

Voranmeldung Telefon 056 / 96 20 08

Zu verkaufen grosses

AQUARIUM

Länge 180 cm, Breite 75 cm, Höhe 60 cm

Telefon 032 / 25 01 62, von 12 bis 13 Uhr

RYOBI

Wurfrollen

haben keinen Vergleich zu scheuen.
Sie bieten einen hohen Gegenwert
für den Preis.

Ueberzeugen Sie sich
im Fachgeschäft!

Engros-Verkauf Schweiz:

W. Stucki AG, 3600 Thun 7

---

migasol imprägniert zuverlässig und dauerhaft

migasol der ideale Schutz vor Wasser, Öl und Schmutz

New

Migasol flüssig
in neuer Qualität und
Grosspackung à 500 ml

für Textilien

für Leder
und
Wildleder

Giftklasse 5 S. Warnung auf der Packung beachten.

Airwick AG, Basel

Die montierten Haken von VMC

sind eine wirkliche Vernunftlösung: Wenige, aber den schweizerischen Verhältnissen ideal angepasste Hakenformen, eine feine und sehr saubere Montage, praktische Aufmachung und — eben — ein sehr vernünftiger Preis!

Montierte VMC-Haken gibt es sowohl für die ganz feine Concours-Fischerei, für den Wurmspezialisten wie für den Petri-Jünger, der einen kräftigen, geschmiedeten Haken wünscht.

VMC-Haken finden Sie in den meisten Fachgeschäften. Erkundigen Sie sich danach!

VMC

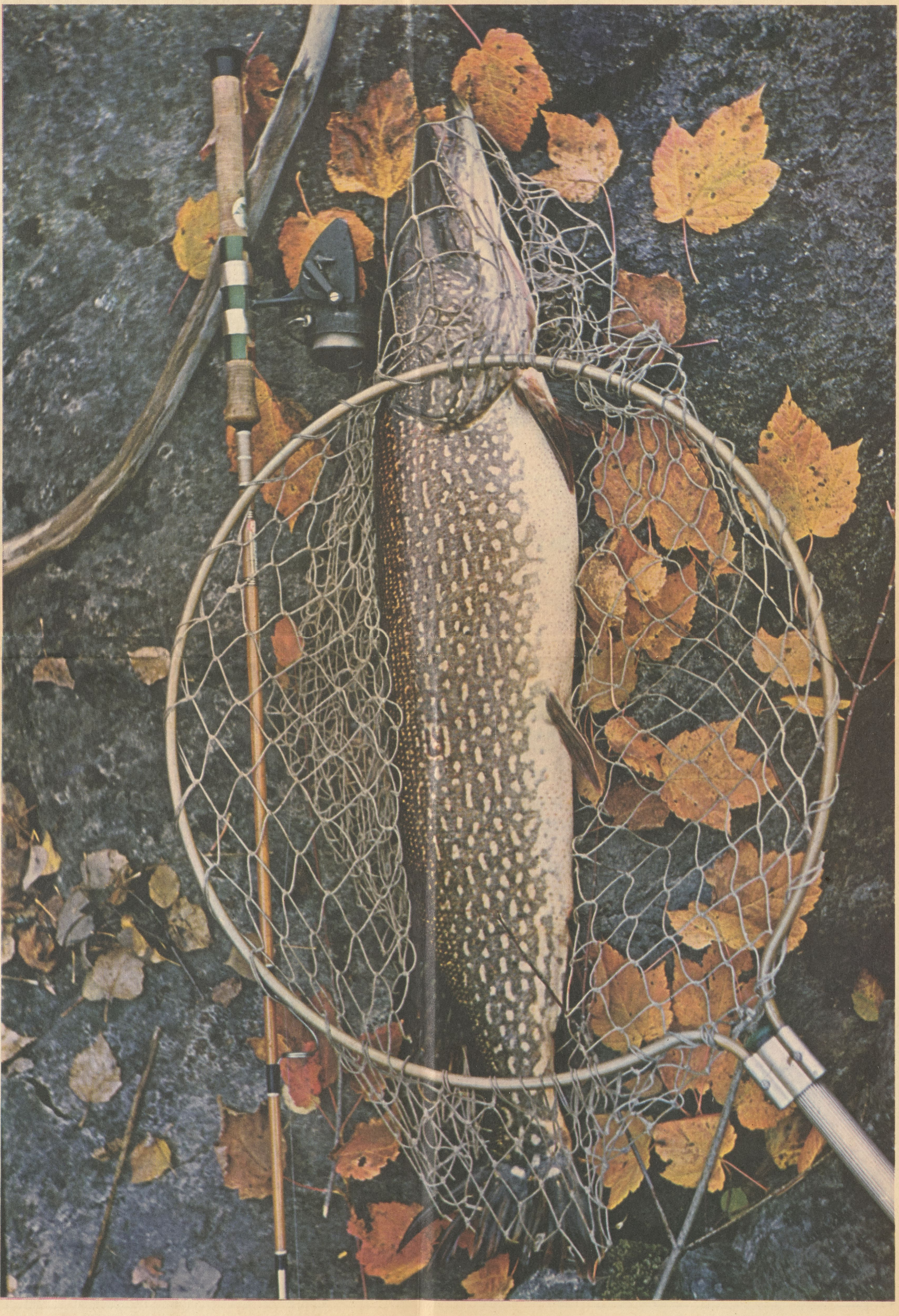
STUCKI THUN

W. Stucki AG
3600 Thun 7

(Nur Engros-Verkauf)

Bild George Silk «Das grosse Anglerbuch»

Hechtposter



J Stor
[1980]

THE SOUTHWESTERN NATURALIST 25(1):51–66 JAN. 30, 1980

HABITAT PARTITIONING IN THE FISH COMMUNITY OF A SOUTHWESTERN RIVER

WILLIAM J. MATTHEWS
AND
LOREN G. HILL

Biological Station and Department of Zoology, University of Oklahoma, Norman, OK 73019

ABSTRACT. Patterns of habitat partitioning and spatial overlap are documented for the fishes of an environmentally unstable southwestern river. *Notropis lutrensis* (red shiner), *Notropis girardi* (Arkansas River shiner), *Hybognathus placitus* (plains minnow), and *Gambusia affinis* (mosquitofish) numerically dominated the fish fauna; few centrarchids or other large species were present. While the dominant species showed some spatial segregation at most times, their habitat use was transitory, changing as environmental conditions changed. The dominant species made wide use of the available habitat during mild environmental conditions and constricted habitat use when physico-chemical conditions were potentially stressful. Species associations were also transitory; no species pairs consistently exhibited strong spatial overlap. Habitat partitioning thus appears less structured in this stream than in more stable environments that have been studied. The fish fauna was characterized by ecologic plasticity, with the most successful species showing marked habitat flexibility.

The South Canadian River in central Oklahoma, like many rivers of the southern Great Plains, is wide and shallow, with seasonal extremes of discharge. Hefley (1937) described the stream thusly: "Probably no more ecologically dynamic region exists: the seasonal, diurnal, and yearly fluctuations of meteorological factors are great and sudden; the course of the river changes with each succeeding rain and the shifting sand . . . is constantly being moved by wind and water." In such a stream, physico-chemical variables like temperature, salinity, and dissolved oxygen fluctuate widely, and may limit the fish fauna (Echelle et al. 1972; Matthews and Maness, in press), or strongly influence microhabitat selection by fishes (Matthews and Hill 1979).

Partitioning of space, which is important in many animal communities (Schoener 1974), has been documented in freshwater fish assemblages by Moyle (1973), Mendelson (1975), Werner and

Hall (1976), Hall and Werner (1977), Werner et al. (1977, 1978), and Baker and Ross (pers. commun.). However, these studies described microhabitat segregation among fishes inhabiting relatively stable environments in comparison to the South Canadian River. Zaret and Rand (1971) described habitat partitioning among fishes in a fluctuating tropical environment, but provided no quantitative microhabitat data. Harrell (1978) documented changes in habitats of West Texas stream fishes after a major flood, but did not distinguish between microhabitats within his collecting localities. Patterns of microhabitat partitioning among the fishes of an environmentally unstable Southwestern river have not been quantified until now.

This study documents microhabitats of the four dominant fish species of the South Canadian River during an annual wet-dry cycle: *Notropis lutrensis* (red shiner), *Notropis girardi* (Arkansas River shiner), *Hybognathus placitus* (plains minnow), and *Gambusia affinis* (mosquitofish). We specifically asked the following questions: (1) Did the dominant species use microhabitats differing physicochemically? (2) Was microhabitat partitioning among the dominant species consistent despite environmental fluctuation? (3) Were species associations permanent? (4) Were there any patterns of habitat use by the fish assemblage as a whole that had adaptive significance?

STUDY AREA. The study site (described in Matthews and Hill 1979) comprised a 600 m segment of the South Canadian River near Norman, Oklahoma, and the lowest 700 m of Pond Creek, a tributary. The river frequently changed course over the unstable sand of the riverbed, and was not deeper than 1.2 m during our study. There were no permanent riffles or pools in the study site, although deeper water and shade were usually found at one side of the riverbed where banks were steep and underbrush and trees were dense. Pond Creek was approximately 10 m wide, with relatively permanent banks bordered by tall grasses and trees. The creek was not deeper than 1 m; bottoms varied from sand mixed with algae and detritus to mud. No permanent riffles were found in the creek, but backwater pools existed. Rooted macrophytes were absent from both streams; algae mats were common in the creek and were noted in the river in October. Both streams were easily seined as few snags or other obstructions were present.

The South Canadian River, like most streams of the Great Plains, has an annual wet-dry cycle, with high water in winter and spring. Evaporation reduces the main river to pools connected by scant flow during most summers; this situation persists until autumn or winter rains. In our year of study the pattern was typical, except that autumn rains were late, and low water continued during

Amer Midland Natural
J Stor
1981
105:1

Tolerance of Headwater vs. Mainstream Fishes for Abrupt Physicochemical Changes

WILLIAM J. MATTHEWS[1] and JOHN T. STYRON, JR.
Department of Biology, Roanoke College, Salem, Virginia 24153

Abstract: A headwater cyprinid (*Phoxinus oreas*) of the Roanoke River drainage (Virginia) was compared to three mainstream cyprinids (*Notropis ardens, N. albeolus* and *N. cerasinus*) for tolerance of abrupt changes in dissolved oxygen, temperature and *p*H. A darter common in the headwaters (*Etheostoma flabellare*) was compared to two mainstream darters (*E. podostemone* and *Percina roanoka*) for tolerance of low oxygen. In all interspecific comparisons, species characteristic of intermittent headwaters were more tolerant than those restricted to the more environmentally stable mainstream. *Etheostoma flabellare* from intermittent headwaters were more tolerant of low oxygen conditions than conspecifics from the river mainstream.

Introduction

Many researchers since Shelford (1911) have documented longitudinal zonation in the distribution of stream fishes. Intermittent headwaters, which are physicochemically more variable than mainstreams (Thompson and Hunt, 1930; Neel, 1951; Harrel *et al.,* 1967; Hynes, 1970; Whiteside and McNatt, 1972; Tramer, 1977) are typically inhabited by only a few species. These fishes have been presumed more tolerant of fluctuating environmental conditions than mainstream species (Thompson and Hunt, 1930; Metcalf, 1959; Harrel *et al.,* 1967), but despite a voluminous bioassay literature (Committee on Water Quality Criteria, 1972; Davis, 1975; Coutant, 1977) no published studies have been designed to test this hypothesis.

In the upper Roanoke River drainage of western Virginia, *Notropis ardens* (rosefin shiner), *N. albeolus* (white shiner), *N. cerasinus* (crescent shiner), *Etheostoma podostemone* (riverweed darter) and *Percina roanoka* (Roanoke darter) are common in lower parts of tributaries and in the main river, but do not occupy headwaters (Cairns *et al.,* 1971; Hambrick, 1973; Jenkins, 1979). In contrast, *Phoxinus oreas* (mountain redbelly dace) is one of the most abundant cyprinids in headwaters of the drainage, but is uncommon or absent in the river mainstream. *Etheostoma flabellare* (fantail darter) is abundant from extreme headwaters to the river mainstream throughout the drainage. Such a distribution of these species in Mason Creek, a tributary of the Roanoke River at Salem, Virginia, was documented by Jenkins and Freeman (1972) and was further substantiated by our field collections 1977-1979.

We tested the hypothesis that fish species of intermittent headwaters are more tolerant of abrupt physicochemical change than species that are restricted to mainstreams. We also asked if intraspecific differences in oxygen tolerance existed between headwater and mainstream populations of the widely distributed *Etheostoma flabellare.* This study also provides the first reports of physicochemical tolerances of the species studied, with the exception of *E. flabellare* for which oxygen and thermal tolerance has been reported (Kowalski *et al.,* 1978; Ultsch *et al.,* 1978).

Description of the Area

Jenkins and Freeman (1972) provided a complete physicochemical description of Mason Creek. It is an upland stream of the Ridge and Valley physiographic province with gravel, rubble and bedrock substrates, but with no differences in substrate type that would account for longitudinal zonation of fish species. Within the portion of Mason Creek that we studied, stream gradient is relatively uniform (ca. 6.6 m/km). Width in the headwaters varies from 2-5 m, and riffle-pool zonation is evi-

---

[1] Present address: University of Oklahoma Biological Station, Kingston 73439.

dent. The headwaters cease to flow during the summer (Jenkins, 1979), and water is then found only in shallow, isolated pools. The surrounding mountainsides are heavily forested, and much leaf litter is found in headwater pools. The headwaters flow over noncalcareous shales and sandstones; thus the water is poorly buffered (Total alkalinity, 6-12 ppm) (Jenkins and Freeman, 1972). The lower 6 km crosses calcareous strata, increasing the buffering capacity of the stream.

The Roanoke River in the vicinity of Salem is 20-40 m wide, with bottoms of gravel, rock rubble and some silt. Flow is continuous. In the river above Salem we have never found dissolved oxygen below saturation and the river (Total alkalinity, 121-222 ppm) is better buffered than is upper Mason Creek.

Although no long-term water quality records exist for Mason Creek, R. G. Burnley, director of field studies for the West-Central Regional Office of the Virginia Water Control Board (pers. comm.), indicates that temperature, *p*H and dissolved oxygen fluctuate more in upper Mason Creek than in the mainstream of the Roanoke River, and numerous other lines of evidence support the assumption that Mason Creek headwaters are less physicochemically stable than the river. Mason Creek headwaters are markedly affected by drought, and it is one of the first streams of its size in the area to cease flowing in the summer (Jenkins, 1979). The headwaters then consist of shallow pools that typically are exposed to direct insolation and often contain much filamentous algae and detritus. Due to the small volume of water in the headwater pools, temperature changes can be rapid. Photosynthesis and detrital respiration can rapidly alter *p*H of the poorly buffered water, and respiration likely results in oxygen depletion in the nonflowing pools. Throughout the year, upper Mason Creek is less physicochemically stable than the river. During 1 week in December 1977, midday temperature at one creek location changed 4 C, while the river changed only 0.2 C. In October 1979, temperature at one creek location decreased 11 C in 4 days; we never found such rapid change in the temperature of the river mainstream. A survey of 21 mainstream river locations June-August 1977 (Virginia Water Control Board memo) showed a *p*H range of 1.1 units, and eight river locations surveyed September 1978 (Dickson, 1979) ranged only 0.5 *p*H units. In contrast, *p*H at one upper creek location varied 1.6 *p*H units in 31 days October-November 1979, while three upper creek locations collectively had a range of 2.1 *p*H units. R. G. Burnley (pers. comm.) indicates that leaching of organics from leaf litter, combined with low buffering capacity, likely causes such *p*H fluctuations in the Mason Creek headwaters.

METHODS

December 1977.—We seined *Phoxinus oreas* from upper Mason Creek (11.1 C) and *Notropis ardens, N. albeolus* and *N. cerasinus* from the Roanoke River (9.2 C) near Salem. Fish were held in an environmentally controlled room (LD 12:12) for 48 hr at 16 C prior to *p*H and oxygen tests, and for 1 week at 15 C before temperature tolerance tests. The 2-day holding period prior to *p*H and oxygen tests is sufficient to allow physiological adjustment of fish to laboratory *p*H conditions (Eddy, 1976; Wood and Caldwell, 1978), and 1 week is the recommended conservative holding period for upward thermal acclimation (Richards *et al.,* 1977), which occurs more rapidly than downward thermal acclimation (Hutchison and Maness, 1979). Fish were housed in 40-liter plastic pails in aged tap water with continuous filtration and aeration and fed Tetra-min once daily, but not fed on the day of tests. No significant mortalities occurred during the holding period, and none of the species showed adverse effects from handling. Dissolved oxygen was kept at air saturation; *p*H ranged from 7.3 - 7.5 during acclimation for *p*H and oxygen tests and from 7.8 - 8.2 during acclimation for thermal tests. Fish ranged from 27 - 80 mm in standard

1981

TAYLOR DRAW RESERVOIR: AQUATIC BIOLOGY ASSESSMENT

Robert J. Behnke
Oct. 1981

The Affected Environment

The upper White River drainage is typical trout stream habitat to below the town of Meeker. As the river progresses westward, gradient declines and it becomes a wide river carrying a heavy sediment load, mainly over a shifting sand substrate, and it is subjected to great fluctuations in flow and temperature (to 80° F and more). These are the habitat characteristics of the river in the proposed reservoir site and below.

Stimulated by the possibility of oil shale development and concomittant environmental changes, considerable study has been devoted to the fish and invertebrate fauna of the White River in recent years. Much of this information was summarized by Carlson et al. (1979) and further reviewed and updated in EIS' on the Moon Lake Power Plant Project and the White River Dam (Utah) Project, both released in 1981. These sources, and others cited, provide an adequate information base to assess the proposed Taylor Draw Reservoir impacts on aquatic biology. The U.S. Fish and Wildlife Service is currently studying endangered fish species in the White River.

Aquatic Wildlife

a. Plants and invertebrates

The primary source of energy in the White River (primary production) is from diatoms (unicellular algae) attached to hard substrate (mainly rock). Some macrophyte vegetation occurs sporadically in protected silt bottom areas with little or no current velocity (*Potamogeton*, *Ranunculus*, *Elodea*). Filamentous algae (*Spirogyra* and *Ulothrix*) may occur during low flow periods of late summer in areas with extensive rocky substrate. Due to high turbidity (blocking light penetration necessary for photosynthesis) and particularly the influence of the predominately sandy substrate, plant production (primary production) in the White River of the proposed reservoir site area and below is low. This situation is analagous to what I found in Fountain Creek, Colorado, where despite high nutrient levels, plant production (and invertebrate production) is extremely low, limited by the physical habitat (primarily the substrate) (Behnke 1980).

The limited plant production and lack of large areas with habitat diversity, limits invertebrate abundance and diversity.

The study by Carlson et al. (1979) sampled the White River for invertebrates in several sites from Rio Blanco Lake to Rangely. Some data on substrate composition is given in their Table 46. The abundance and diversity of aquatic insects varied in different sampling periods but the Shannon-Weaver Diversity Index for White River samples was less than 3.0, characteristic of a "stressed" or "degraded" environment.

Species of all of the major orders of aquatic insects were found. Larvae of mayflies (Emphemeroptera) were most abundant, followed by caddis larvae (Trichoptera), "true" flies (mainly midge larvae of the order Diptera) and stonefly larvae (Plecoptera). Other invertebrate animals found in the White River include two species of snails

[Excess nutrients]
1991

EFFECT OF EUTROPHICATION ON FISHERIES

G. Fred Lee and R. Anne Jones

Department of Civil Engineering
Colorado State University
Fort Collins, CO 80523

INTRODUCTION

The overall degree of eutrophication of a waterbody, which is determined by its aquatic plant nutrient loads, has a significant impact on the waterbody's fisheries resource. From a positive point of view, for many waterbodies an increase in the aquatic plant nutrient load results in increased sustained fish yield. On the other hand, there are a number of negative impacts on fisheries resources associated with increased aquatic primary production. This paper reviews the current state of knowledge on the impact of eutrophication on fisheries resources and presents a eutrophication control policy that the authors feel should be followed in management of excessive fertility as it relates to fisheries resource management.

CHARACTERISTICS OF EUTROPHICATION

Eutrophication can be generally characterized as the process of increasing the aquatic plant and other biomass of a waterbody. Lakes and other surface waters are frequently classified in one of two categories, oligotrophic and eutrophic. Although the exact meaning of these two terms depends on the user, it is generally agreed that oligotrophic waterbodies are relatively unproductive and receive comparatively small amounts of aquatic plant nutrients, while eutrophic waterbodies are highly productive in

---

Prepared at the request of the American Fisheries Society Water Quality Committee. The attached is a preprint of the paper which is currently under review. If you have any questions or comments about any aspect of the paper, please contact the authors. It is expected that a slightly revised version of this paper will be published by the American Fisheries Society.

terms of plants and animals and experience high influxes of aquatic plant nutrients. It is generally found that the more eutrophic waterbodies tend to experience water quality problems which impair their use as domestic and industrial water supplies and for recreation. The most readily observable feature of eutrophic waterbodies is the luxuriant growth of aquatic plants. In shallow nearshore areas, this growth is manifested as large crops of attached or floating aquatic macrophytes and attached algae. Occasionally high populations of planktonic algae will be found in these areas, usually due to wind-induced currents channeling them to shore. In open waters, eutrophication is usually manifested as planktonic algal growth and in some cases floating aquatic macrophytes.

EFFECTS OF EUTROPHICATION ON FISHERIES RESOURCES

Eutrophication of a waterbody can have a number of effects on the quantity and quality of fish within the waterbody. A summary of these impacts is presented below.

QUANTITY OF FISH

One of the most pronounced effects of eutrophication on the fisheries resource of a waterbody is a general tendency for increased fish stock with increased levels of primary production. This was demonstrated by Oglesby (1977), who reviewed the relationships between fish yield and planktonic algal productivity and between fish yield and planktonic algal biomass as measured by chlorophyll.

Several years ago, Vollenweider (1968, 1976) suggested that planktonic algal biomass as measured by chlorophyll could be correlated with the phosphorus load to the waterbody normalized by its mean depth and hydraulic residence time. During the past five years, under the leadership of R. Vollenweider and the auspices of the Organization for Economic Cooperation and Development (OECD), a multi-nation study has been conducted on nutrient load and associated eutrophication response as measured by planktonic algal chlorophyll. The nutrient load-eutrophication response relationships for approximately 200 waterbodies located in North America, Western Europe, Japan, and Australia have been examined. Within the U.S., approximately 40 waterbodies were included in this study; a number of reports summarizing the results of the US OECD eutrophication study have been prepared (Rast and Lee, 1978; Lee et al., 1977; and Lee et al., 1978c). The important conclusion of the U.S. study is that the above-mentioned Vollenweider nutrient load-eutrophication response relationship is applicable to a large number of U.S. waterbodies. Following the approach developed by Vollenweider and using the US OECD eutrophication study data base, Rast and Lee developed relationships between normalized P load and Secchi depth, and between normalized P load and hypolimnetic oxygen depletion rate. Figure 1 presents these relationships. The abscissa for these three relationships is $(L(P)/q_s) / (1 + \sqrt{\tau_\omega})$ where L(P) is the annual areal P load in mg $P/m^2/yr$, τ_ω is the hydraulic residence time (filling time) in years, and q_s is equivalent to the waterbody mean depth divided by the hydraulic residence time, in m/yr. This abscissa term is equivalent to the mean, steady state P concentration in the waterbody. While the total OECD eutrophication study data base has not yet been published, preliminary examination of these data show that they obey the same relationships developed based on the US OECD data.

It is possible to combine Figure 1 with Oglesby's (1977) results to develop a relationship between the normalized P load to a waterbody and the fisheries yield in the waterbody. This relationship is presented in Figure 2. Oglesby's (1977) relationship was developed from a relationship between Secchi depth and fish yield and between Secchi depth and chlorophyll. Since Oglesby's data base for re-

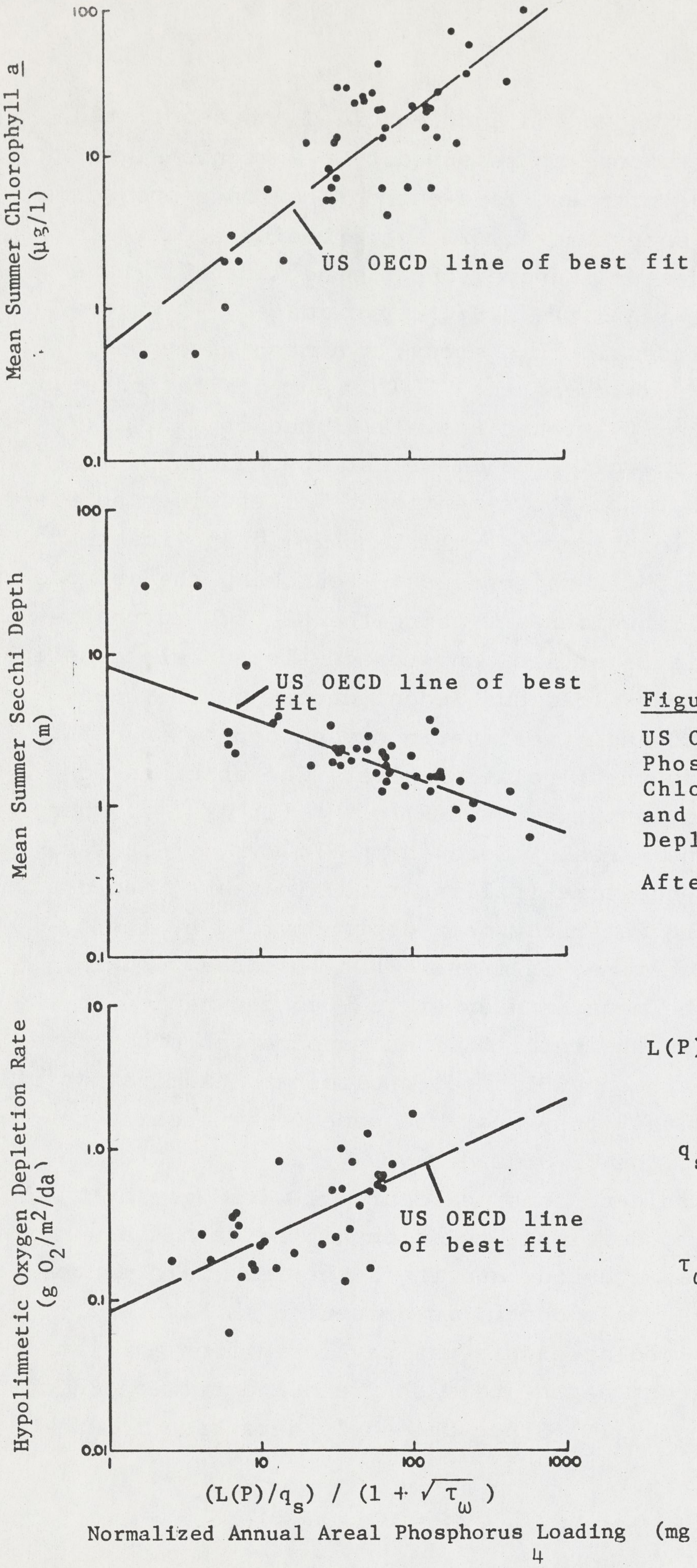


Figure 1.

US OECD Data Applied to Phosphorus Loading - Mean Chlorophyll a - Secchi Depth, and - Hypolimnetic Oxygen Depletion Rate Relationships

After Lee *et al*. (1978c).

KEY

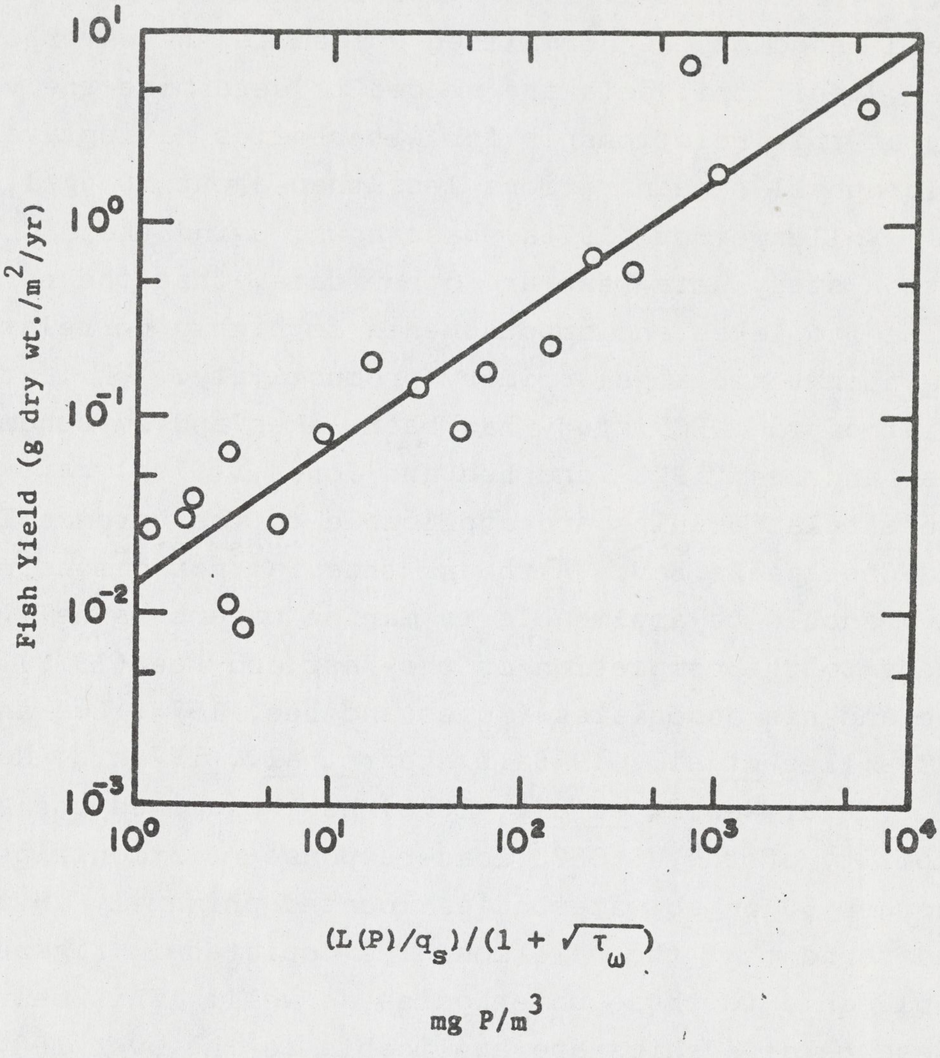
$L(P)$ = areal annual phosphorus load ($mg\ P/m^2/yr$)

q_s = mean depth ÷ hydraulic residence time (m/yr)

τ_ω = hydraulic residence time (yr)

Figure 2.

Relationship between Phosphorus Load and Fish Yield



Line of best fit:

$$\log \text{Fish Yield} = 0.7 \log [(L(P)/q_s)/(1 + \sqrt{\tau_\omega})] - 1.86$$

$$(r^2 = 0.86)$$

Based on data from Oglesby (1977) and Rast and Lee (1978).

lating Secchi depth to chlorophyll was limited compared to that developed by Rast and Lee which included over 100 data sets from the literature, Figure 2 was developed based on Oglesby's fish yield-Secchi depth relationship and Rast and Lee's normalized P load-Secchi depth relationship. Through this relationship it is now possible to estimate the fish yield based on the normalized P load to the waterbody. However, additional data are needed to determine the variability of this relationship for waterbodies having average chlorophyll concentrations less than about 50 µg/l.

Vollenweider (1979a) has shown, using the OECD eutrophication study data base and other data, that the normalized P load to lakes and impoundments is highly correlated with the planktonic algal primary productivity. While the focal point of the OECD study has been lakes and impoundments, Rast and Lee (1978) and Lee and Jones (1979b) have shown that these relationships are applicable to the Potomac Estuary and Chesapeake Bay. Although thus far not demonstrated, they should be applicable to marine waters as well. Subsequent to the completion of the Rast and Lee (1978) work, Lee and his associates (Jones and Lee, 1978; Lee and Jones, 1978a; Lee _et_ _al_., 1978a,b; Lee _et_ _al_., 1979a,b; Nambu _et_ _al_., 1978; Newbry _et_ _al_., 1979) have examined the applicability of the US OECD load-response relationships to another 60 or so waterbodies located primarily in the U.S., and found that the relationships depicted in Figure 1 are applicable to these waterbodies as well. This means that these relationships are applicable to the over 100 U.S. waterbodies to which they have been applied. The additional work by Lee and his associates has extended the geographical distribution of waterbodies that have been examined using this approach to all parts of the U.S., and most importantly have clearly demonstrated that there is no significant difference in the load-response relationships for natural lakes and reservoirs. It is now possible, as a result of Vollenweider's original concepts and the OECD study, as well as the work of Oglesby, to relate P load to a waterbody (lake or impoundment) to the waterbody's planktonic algal chlorophyll, planktonic primary production, water clarity that is controlled by planktonic algae, hypolimnetic oxygen depletion rate, and fish yield.

As discussed by Rast and Lee (1978), there are a number of important constraints governing the use of these types of relationships. First and foremost, these relationships should be applicable only to waterbodies in which the maximum planktonic algal biomass during the summer growing season is limited by phosphorus, and in which the hydraulic residence time during the summer growing season is two weeks or more. Further, it is only applicable to waterbodies in which the P load is primarily manifested as planktonic algal chlorophyll. It would not be applicable to those shallow lakes and reservoirs in which the P load is used primarily to support macrophytes and attached algae. These relationships would also not be applicable to waterbodies where allochthonous detritus provides the major food source for zooplankton and higher trophic level organisms, nor would they be applicable to waterbodies in which fish reproduction is affected by toxic chemicals or lack of adequate habitat.

QUALITY OF FISHERIES

Eutrophication can also significantly affect the types of fish present in a waterbody. Generally, highly eutrophic waterbodies tend to have dominant populations of fish such as carp and other rough fish which are deemed by most North Americans to be less desirable. While the exact mechanism of this change from more desirable fish to rough fish with increasing fertility is not well understood, it appears to be related to such factors as increased turbidity caused by increased amounts of phytoplankton reducing the grazing ability of carnivorous fish. This situation tends to be autocatalytic since once carp and other rough fish become dominant components of the fish population, they often significantly decrease the overall water clarity through their routing actions in the waterbody sediments.

Some highly eutrophic waterbodies also tend to produce large populations of stunted pan fish. This may be the result of inadequate predation on these fish arising from the inability of predators to see them due to increased planktonic algal and suspended sediment turbidity. Based on the experience of the authors, stunted pan fish populations tend to occur in waterbodies with summer average Secchi depths of less than 1m, which generally corresponds to a summer average chlorphyll concentration of 40 to 50 µg/l.

Another effect of eutrophication on the quality of fish is the loss of cold water fish from thermally stratified waterbodies which lose the oxygen from their hypolimnia. This oxygen depletion is generally caused by increased amounts of planktonic algae in the surface waters, which settle through the thermocline and become a source of biochemical oxygen demand (BOD) in the hypolimnetic water-column and sediments. For some waterbodies, ammonia present at the onset of thermal stratification exerts a sufficient oxygen demand through nitrification reactions to significantly reduce the dissolved oxygen concentration in the hypolimnion. Newbry _et_ _al_. (1979) found for Cherokee Reservoir, part of the Tennessee Valley Authority reservoir system, that about half of the hypolimnetic oxygen depletion is due to phytoplankton death and decay, the other half being due to nitrification. There have been a number of notable examples of significant losses of valuable fisheries apparently due to increased phosphorus load to a waterbody resulting in increased phytoplankton growth with an associated increased hypolimnetic oxygen depletion rate. The loss of the cisco population in Lake Mendota, Madison, Wisconsin, described by Frey (1955) is one example of this.

Conway (1972) examined oxygen depletion rates for Lake Mendota and found that Frey's hypothesis was in accord with the eutrophication history of this lake. This case is not one in which the hypolimnion at one time in history remained oxic throughout the summer and then became anoxic as a result of increased nutrient loads. As discussed by Conway (1972), the hypolimnion of this lake has gone anoxic every summer since before the turn of the century; the massive cisco die-offs did not occur until the 1930's to 1940's. Frey proposed that the cisco were surviving in a microhabitat just below the thermocline. This area had sufficient oxygen and a suitable temperature to keep the cisco alive during periods of anoxia in the hypolimnion. The oxygen was maintained prior to the 1930's by a balance between the rate of 0_2 diffusion through the thermocline from the epilimnion to the hypolimnion and oxygen depletion due to bacterial respiration. The cisco started to die off when increased urban and agricultural activities within the Lake Mendota watershed resulted in an increase in P load to the waterbody. The additional algae produced increased the 0_2 demand of the water immediately below the thermocline to the point where the cisco were no longer able to survive.

It is sometimes alleged that the impact of eutrophication on Lake Erie has been the loss of cold water fish due to the depletion of oxygen in the hypolimnetic waters. Welch (1978) reviewed this topic and presented considerable evidence that the primary cause of the decline of more desirable fish in Lake Erie has been overfishing. There are a number of recently completed studies such as Lee and Jones (1979a) and Vollenweider (1979b) which show that in order to maintain 4 mg/l dissolved oxygen in the hypolimnion of Lake Erie in all years, the P load would have to be about 1,000 to 2,000 mt P/yr. Since the current load is on the order of 20,000 mt P/yr and the P load can readily and economically be reduced by only 5,000 to 7,000 mt/yr, it appears unlikely that cold water fisheries will ever be maintained in the Central Basin of the Lake. P loads prior to the turn of the century were likely sufficient to cause the hypolimnion of Lake Erie to become anoxic in some years. It is therefore concluded that the rapid eutrophication of the surface waters of Lake Erie during the past 20 years has not had a significant impact on the deoxygenation of the hypolimnion of this lake and therefore this eutrophication has likely had limited impact on the cold water fishery during this period of time.

It is clear that eutrophication management for optimum fisheries will at times be in conflict with eutrophication management for recreational, domestic and industrial water supply and other uses of the water since increased nutrient loads lead not only to increased fish production but also to decreased water quality in terms of most non-fisheries related uses. For optimum cold water fisheries, there is a balance of having sufficient algal growth for food but not enough to cause detrimental hypolimnetic oxygen depletion. For any waterbody which thermally stratifies and whose surface waters become too warm for cold water fish, there is a maximum P load that will provide the maximum cold water fish yield. This load may be determined from the information provided in Figure 1 and the morphological characteristics of the hypolimnion. As discussed by Lee and Jones (1979a), year to year variations in the position of the thermocline can significantly alter the impact of a particular P load on the extent of hypolimnetic oxygen depletion.

Another aspect of eutrophication which can have a significant effect on the quantity and quality of fish in a waterbody is winterkill. It arises principally in shallow waterbodies which develop an ice cover lasting for several months or more. Under these conditions, respiration of bacteria decomposing the seston, and sediment oxygen demand can cause oxygen depletion under the ice. This is especially important in shallow lakes because of the limited dissolved oxygen reservoir. If there is no snow cover, then light can generally penetrate to the water and allow algal growth and the production of sufficient oxygen to maintain fish. However, should snow cover, especially an early snow cover, substantially reduce or eliminate light penetration, the oxygen concentrations beneath the ice can be reduced sufficiently to kill fish. Eutrophic waterbodies tend to have more frequent occurrence of winterkill due to the greater primary production which serves as a source of energy for the bacteria. While winterkill can result in complete destruction of all fish in a waterbody, the effect is generally to kill the most sensitive, often more desirable fish. This situation promotes the dominance of rough fish such as carp which are generally more tolerant of low dissolved oxygen concentrations.

Winterkill problems can generally be eliminated by aeration of the waterbody. For a relatively small energy input, it is possible to add considerable amounts of dissolved oxygen to the waterbody through a simple diffusion system. Another technique that can be used to add large amounts of oxygen with low energy input is sidestream aeration in which water is pumped from the waterbody to shore where air is added and then the water is returned to the waterbody. In addition to direct absorption of oxygen by the water, these approaches will usually make part of the waterbody ice free and thereby aid in the surface transfer of oxygen from the atmosphere into the water. For those waterbodies prone to winterkill conditions and to developing sufficiently thick coatings of ice to support snow removal equipment, consideration should be given to removing heavy, persistent snow cover so that a substantial part of the ice is essentially snow free, thereby allowing light penetration through the ice.

EFFECTS OF EUTROPHICATION ON MARINE FISHERIES

In general the oceans of the world are nutrient-starved, with the fisheries being limited to a considerable extent by the limited primary production that occurs in them. There are situations, however, where excessive nutrients in coastal marine waters can have a significant deleterious effect on fisheries and water quality, notably associated with the development of "red tide" organisms, usually dinoflagellates. The dinoflagellate blooms in coastal waters can have an adverse effect on fisheries from two points of view. First there is the problem of oxygen depletion as the result of the massive die-off of an algal bloom. The Emilia-Romagna region of Italy on the northwest Adriatic Sea experienced a problem of this type several years ago where nitrogen, apparently primarily derived from agricultural and industrial waste, and phosphorus derived from wastewaters discharged from municipalities located along the coast, resulted in massive phytoplankton blooms in the coastal waters. The oxygen depletion resulting from decomposition of these organisms and the meteorological conditions that existed during the summer, apparently caused fish kills. For further discussion of the Emilia-Romagna situation, consult Lee and Jones (1977) and Lee (1978).

A similar problem occurred along the New Jersey coast in the summer of 1976 when the waters below the halocline in a large region (approximately 10 to 20 kilometers wide and 150 to 200 kilometers long), became anoxic as the result of a die-off of a dinoflagellate bloom. A massive die-off of benthic fish, shellfish, and other organisms occurred in late summer because of these conditions. It appears in this case that the problem was caused by the introduction of excessive amounts of nitrogen compounds which stimulated excessive phytoplankton growth in the surface waters of this region. These organisms died, settled through the halocline and used up the oxygen in the hypolimnetic waters. This type of situation would not be expected to recur in these waters year after year, however. While there appears to be about the same phytoplankton biomass development each year in these waters, the combination of meteorological conditions that occurred in 1976 reducing mixing of nearshore surface waters with offshore surface waters, and mixing of nearshore and offshore hypolimnetic waters resulted in the complete exhaustion of oxygen in near bottom waters and the subsequent death of organisms.

Off the coast of Florida and in the coastal waters of Japan, especially the Seto Inland Sea, as well as in other parts of the world, toxic dinoflagellate blooms have developed, causing fish kills. Japanese fishermen have been particularly impacted by this phenomenon. Millions of kilograms of commercially reared fish (yellowtail) have been lost during single dinoflagellate blooms. From the information available, it is clear that there is need for work to define the relationship between aquatic plant nutrient input to marine waters and the growth of toxic dinoflagellates which can impact fisheries.

EFFECTS OF EUTROPHICATION ON FISHERIES IN RIVERS AND STREAMS

As with lakes, impoundments, and estuaries, more eutrophic rivers and streams would tend to have greater fish yield. However, at this time it is not possible to quantify nutrient load-eutrophication response relationships for flowing waters. One of the primary deleterious effects of eutrophication of flowing waters on fisheries is the diel fluctuation of oxygen concentration. In highly eutrophic streams, dissolved oxygen concentrations can be sufficiently low during early morning hours to be deleterious to fish. This is especially true if there is an additional allochthonous oxygen demand such as from domestic and industrial wastewater sources. Studies need to be conducted to relate aquatic plant nutrient load to eutrophication response in rivers and streams in order to quantify both beneficial and detrimental effects of increased fertility in lotic waters.

CONTROL OF EXCESSIVE FERTILITY AND ITS IMPLICATION FOR FISHERIES

EXTENT OF CONTROL DESIRABLE

As discussed previously, increased fish production is generally associated with greater nutrient loads. At the same time increased nutrient loads can cause detrimental impacts to various aspects of water quality. A conflict exists, therefore, in making a decision on the degree of nutrient load control desirable for a waterbody. However, for any given waterbody there is some "optimum" nutrient load which will provide the greatest fish production with minimum significant detrimental eutrophication-related effects such as loss of cold water fisheries in the hypolimnion, development of stunted fish populations, and impaired quality of water for domestic or industrial water supply and many recreational uses. The overall approach that has generally been used for eutrophication control is to reduce the loads of the growth limiting or potentially limiting nutrient to the waterbody to the maximum extent possible. This will tend to minimize such water supply problems as tastes and odors, increased chlorine demand, shortened filter runs, increased color, and in some situations trihalomethane precursors, and impairment of recreation. As discussed previously, through the OECD eutrophication modeling approach, it is now possible to assess the impact of such load reductions on many fisheries-related qualities, such as the oxygen status of hypolimnetic waters, planktonic algal-related water clarity, and overall fish yield, as well as some characteristics important to water supply and recreational uses such as mean and maximum planktonic algal chlorophyll concentrations. There are a number of more subtle impacts of nutrient load-eutrophication on fisheries which cannot be reliably predicted, such as the point at which fish become stunted and destruction of certain fish habitat. Further research is needed to define the relationship between these effects and nutrient load. Once this is done, it will be possible to better define the trade-offs between fisheries-related water quality and water supply-recreationally desirable water quality, involved in choosing a target nutrient load.

METHODS OF NUTRIENT LOAD REDUCTION

Domestic Wastewaters

Since domestic wastewaters represent a potentially significant source of aquatic plant nutrients to many waterbodies, this source is generally looked to first for control. The most dramatic effects that can be produced by controlling wastewater nutrients would be achieved by complete diversion of the wastewaters out of the waterbody of concern onto land or to downstream waters. The effect on eutrophication-related water quality of this method has been demonstrated in the Madison, Wisconsin lakes and in Lake Washington, Seattle, Washington. While this method can improve water quality, especially for those waterbodies in which nutrients are derived primarily from domestic wastewaters, it can also cause deteriorated water quality in the new receiving waters. In general, this method is not a satisfactory solution to the overall problems of eutrophication. There have been cases where domestic wastewater diversion has allegedly resulted in little or no improvement in water quality, such as Lake Sammamish near Seattle, Washington. Examination of the Lake Sammamish situation shows that such a result would be expected since the magnitude of nutrient diversion was small compared to the total nutrient load.

Since for the majority of waterbodies in the U.S., phosphorus is the element which limits maximum planktonic algal growth in the summer, phosphorus removal from domestic wastewaters is another viable nutrient control method. On the order of 90% of the phosphorus present in domestic wastewaters can be readily removed using iron or alum precipitation techniques for about a quarter of a cent per person per day for the population (> 10,000 people) served. These techniques will reduce the effluent P concentrations from 5-10 mg P/l to 0.5 - 1 mg P/l and are routinely practiced in Sweden, Canada, in the U.S. portion of the Great Lakes basin, and in a number of other areas across the U.S. For some waterbodies there has been discussion of reducing the domestic wastewater P load to on the order of a few tenths of a mg P/l using filtration techniques. As discussed by Lee _et al_. (1979c), before these typically more expensive measures are taken, an assessment must be made of the amount of phosphorus in the additional portion removed, that is available to support algal growth. While much of the phosphorus removed by iron or alum precipitation is readily available to aquatic plants, the remaining portion is largely particulate, associated with iron or aluminum floc. The availability of this P fraction is not yet known.

Phosphorus from use of household laundry detergents at one time comprised a substantial (50 to 60%) portion of the P in domestic wastewaters and was therefore a target for some eutrophication control programs. Due to reductions in the P content and reformulation of household laundry detergents in recent years by the detergent industry, this source currently makes up about 30 to 35% of the P in domestic wastewaters. While several U.S. states and a Canadian Province have imposed restrictions on the percent allowable P in detergent formulations, as discussed by Lee _et al_. (1979c), there have been no documented cases where this action has had a significant impact on eutrophication-related water quality. This would be expected since even in waterbodies in which 50% of the P load was from domestic wastewaters (which is unusually high for most waterbodies), a complete ban on P in detergents would only result in a 15% P load reduction. As demonstrated using the OECD eutrophication model, generally much larger P load reductions are needed before perceivable changes in eutrophication-related water quality are realized.

One of the most significant results of the OECD eutrophication study is that it is now possible to quantify the improvement in eutrophication-related water quality that can be achieved through phosphorus load reduction. Rast *et al.* (1979) examined the reliability of the OECD modeling approach in predicting the impact of altering the P load on water quality as measured by planktonic algal chlorophyll. They found good agreement between the predicted and measured chlorophyll concentrations for 16 waterbodies for which data were available. While in the past, P control programs have been carried out without a resultant improvement in water quality, these types of errors can now be avoided using the OECD eutrophication modeling approach.

For waterbodies which are nitrogen limited, some reduction in the N load can be achieved by domestic wastewater treatment. Removal of ammonia and other nitrogen species can be achieved by ion exchange, ammonia stripping or bacterial nitrification-denitrification, but these processes are often very expensive and can require large scale changes in a treatment plant. Before these procedures are undertaken, other control methods should be investigated. For example, it may be that by controlling the P in the effluent, the waters of concern can be forced to P limitation so P reductions could cause improved water quality.

Diffuse (Non-point) Sources

There is a host of non-point sources of nutrients which generally contribute a substantial portion of the total nutrient load to a waterbody. These include urban drainage and agricultural and other land runoff. Rast and Lee (1978) and Lee *et al*. (1979d) have discussed a procedure whereby the diffuse source total N and P loads to a waterbody can be estimated based on land use. They have developed generally applicable nutrient export coefficients based on the US OECD eutrophication study data on measured nutrient loads and land use for about 40 U.S. waterbodies. Load estimates based on export coefficients and the OECD model can be used as a first step in determining the potential benefits to water quality that may be obtained by controlling certain non-point sources such as by collecting and treating urban drainage, zoning agriculture, and erosion control. However, since these estimates are for total N and total P, caution must be used in assessing the impact of non-point source nutrient control. As discussed by Lee *et al*. (1979c), on the order of 20% of the particulate P from non-point sources is available to support planktonic algal growth in receiving waters. This can roughly be translated to be about 50% of the total P load from these sources. Since non-point source nutrient control programs are considerably more difficult to develop and implement than most point source programs, careful evaluation of the availability of non-point source nutrients must be made and their relative impact on water quality assessed before such measures are implemented. For further information on the procedures that may be used to estimate available P loads to waterbodies, consult Lee *et al*. (1979c).

INTERNAL MANIPULATION

There are a number of in-lake techniques that have been used to reduce the impact of eutrophication on water supply and recreational use of waterbodies. The major control methods of this type and their potential impact on fisheries-related water quality are discussed below. This discussion is based, in part, on the review by Lee (1973).

Aeration

In an attempt to eliminate the problems associated with low-oxygen hypolimnetic water, two forms of in-lake aeration have been practiced. Complete aeration of the waterbody in which the thermal structure of the waterbody is destroyed, will cool the surface waters in addition to providing oxygen to the bottom waters. The hypolimnetic waters, however, are often significantly heated so that depending on the climate of the region, the lake overall can be heated sufficiently so that it would become impossible to maintain a cold water fishery. The other approach used for aeration is hypolimnetic aeration in which the thermal structure of the waterbody is maintained. This approach enables the establishment of a cold water fishery since it provides oxygen to the hypolimnion but does not increase the water termperature. There may be some problems, however, with embolism in fish due to supersaturated nitrogen conditions which can occur in the bottom waters by using air aeration. A method for alleviating this problem is the use of 100% oxygen rather than air as the means of aerating the hypolimnion.

Studies were conducted by the Wisconsin Department of Natural Resources on Cox Hollow Lake to evaluate whether or not whole lake aeration could increase the fish yield of this waterbody, which tended to strongly thermally stratify a few meters below the surface. Since below the thermocline there was complete deoxygenation of the water, the volume of the lake which was available for fish was limited to a relatively narrow band of surface water. Aeration did not result in a discernible increase in fish yield of this waterbody.

Nutrient Removal

One of the more promising techniques for control of excessive fertility in lakes for which it is impossible to control the nutrient input, is the direct addition of aluminum sulfate to the waterbody. This technique has been demonstrated in Sweden, Canada (Ontario), and the U.S. (Wisconsin) to effectively remove phosphorus from the water column by sorption onto the aluminum hydroxide and subsequent precipitation to the sediments. Thus far this technique has proven to significantly reduce algal-related water quality problems without having a significant direct, observable effect on fish. Of course, any time the total production is reduced in a waterbody, the overall fish production that the waterbody will sustain over extended periods of time may also be reduced. However, it is possible that for some waterbodies in which the zooplankter fish food source feeds primarily on allochthonous detrital material, reduction in the amount of planktonic algae will not affect fish populations. Reduction in planktonic algal turbidity could result in increased macrophyte growth perhaps increasing fish nursery grounds.

Harvesting

Aquatic plant harvesting is a method of removing some of the problems of excessive fertility in some waterbodies, which is widely practiced in several southern states for the control of water hyacinths. In other parts of the country, submerged macrophytes and attached algae are also effectively harvested by mechanical means. While generally this approach does not significantly alter the nutrient content of the waterbody, it does improve the usability of the water for various recreational purposes, including fishing. Aquatic weed harvesting should be practiced to the minimum extent necessary to permit the use of the waterbody to the extent desired, since over-harvesting can lead to the destruction of fishery habitat and to the production of planktonic algal blooms. There have been a number of situations where complete destruction or removal of aquatic macrophytes has resulted in the production of large scale planktonic algal blooms with their associated water quality problems.

There are several reports in the literature which indicate that attached macrophytes "pump" phosphorus from sediments to the overlying waters. It is possible that in some waterbodies, this pumping action would tend to stimulate planktonic algal and floating macrophyte growth to a significant extent beyond that which would occur if the macrophyte populations were substantially reduced. There is need for further work on the role of attached macrophytes in making P available in the water column which would not be available otherwise. Such work could lead to further refinement of the management strategy for macrophytes in lakes which would optimize fish habitat and minimize eutrophication-related water quality problems.

Chemical Treatment

The use of herbicides or other chemicals for the control of excessive aquatic plant growths can be an effective, although usually expensive way to minimize the problems of excessive fertility in waterbodies. This approach can have significant adverse effects on fisheries. Excessive use of chemicals, such as copper sulfate, can result in toxicity to fish. Also, the widespread use of chemicals of this type throughout a whole waterbody can result in a sufficiently large scale die-off of aquatic plants so as to deplete the oxygen resources of the waterbody through the decay of the vegetation and a fish kill could result. It is imperative that any herbicides be used in such a manner so as to minimize or eliminate the direct adverse effects on fish such as toxicity, and indirect effects such as oxygen depletion. This generally involves limiting the use of the chemical to only parts of the waterbody at a particular time.

A unique aspect of the use of chemicals which would have an adverse effect on fisheries for the control of aquatic organisms is the use of TFM in the Great Lakes. This chemical is highly specifically toxic to sea lamprey larvae. It has been shown to be highly persistent in aquatic environments with the result that questions have been raised about its potential hazard to other organisms as a result of long-term buildup. A recently completed review of this topic by Thingvold and Lee (1979) has shown that the probability of TFM creating a hazard to fisheries as a result of its use for sea lamprey control is very remote. The benefits of the use of this chemical far outweigh any potential hazard associated with it, based on the current state of information on the use and the characteristics of the chemical.

Biological control

One of the potentially important techniques for controlling excessive fertility in waterbodies which as yet has not been properly documented in terms of its effectiveness, is the use of plant-eating fish or other animals. Since each type of aquatic plant may have a significantly different impact on water quality and since fish and other organisms will selectively graze certain types of aquatic plants or zooplankton which selectively graze certain types of plants, then the manipulation of fish populations can have a significant impact on the way in which the overall primary production of a waterbody is manifested. It is important to emphasize that it is the aquatic plant nutrients which control the overall fertility. The role of zooplankton and in turn, fish, is to influence how this fertility is manifested. There are some, such as Shapiro, who advocate that through the control of fish populations, one can significantly alter water quality in a waterbody. The basic premise is that by removing fish that eat zooplankton and thereby allowing the zooplankton to develop to the maximum extent possible, it should be possible to graze off many of the phytoplankton which have an adverse effect on water quality. While intuitively this approach appears to be feasible, its effectiveness on a whole lake basis remains to be demonstrated. It has no practical applicability, however, to the management of fisheries and it would likely be vigorously opposed by fisheries managers and fishermen.

One of the most notorious examples of attempts to control aquatic plant populations through the use of fish was the importation of grass carp. The introduction of this fish in the United States has caused considerable controversy among fisheries managers as to whether it would effectively control excessive growths of aquatic plants and whether other problems would develop because of its presence in a waterbody. At this time it has not proven to be an effective, ecologically sound way to control excessive fertility. Further, the effects of this fish on other fish populations are still largely unknown.

State fisheries managers are well aware of the potential impact of the control of rough fish population on the aquatic plant numbers and types in waterbodies. Rough fish such as carp stir up the bottom sediments thereby causing the water to be turbid and limiting the growth of attached algae and macrophytes. With the removal of these fish, the water becomes clearer and can promote the growth of these aquatic plants. It does not appear, however, that the overall production-photosynthesis is drastically changed because of the addition or removal of rough fish. It is generally believed that the effect is to shift from planktonic algal to macrophyte production or vice-versa. The reintroduction of carp into a waterbody can readily convert the waterbody from being "weed-choked" back to a relatively weed-free one with extensive planktonic algal blooms. A possible exception to this would occur for waterbodies which become sufficiently turbid due to stirring of sediments into the water column so that light limitation precludes limitation of maximum algal biomass production by nutrients. The overall impact of changing from macrophyte to planktonic algal populations or the reverse on overall fisheries is not well known. It can be speculated that the complete elimination of the submerged macrophyte population will greatly reduce the fisheries habitat for small fish and eliminate potential breeding areas.

Another animal which appears to be effective in harvesting macrophytes is the manatee. The use of this animal for this purpose is restricted in the U.S. to the tropical-semi-tropical waters of Florida.

Dredging

A procedure that has been used for eutrophication control is dredging of waterbody sediments. While this procedure will not likely have a major impact on nutrient release from the sediment, it will increase the depth of the waterbody. This can decrease the area suitable for attached aquatic macrophyte growth and result in increased amounts of planktonic algal growth. The use of dredging should be minimized in waterbodies in which fisheries resources are of concern because of this effect.

Water Level Management

Additional management options that are sometimes available for impoundments are water level management and controlled flushing. Through manipulation of the depth of the waterbody and the hydraulic residence time, the planktonic algal chlorophyll production per unit P load can be altered. This is demonstrated in the OECD eutrophication model in which it is shown that the P load as normalized by mean depth and hydraulic residence time is related to the planktonic algal chlorophyll concentration, Secchi depth (water clarity), hypolimnetic oxygen depletion rate, and fish yield. Also manipulation of water levels can significantly alter macrophyte and attached algae production.

314 A

As a result of the initiation of the Clean Lakes Program developed in response to Section 314 A of Public Law 92-500, considerable work is under way to develop control programs for excessively fertile waterbodies. These control measures are typically focused on reducing impacts of eutrophication on use of the water for water supply, recreation, and as an asthetic asset. While eutrophication control programs sometimes have some positive impact on fishery resource-related water quality, for example through reducing hypolimnetic oxygen depletion, optimizing eutrophication-related water quality for fisheries has not typically been a focal point of 314 A activities. As discussed above, eutrophication control techniques may result in large changes in water quality as measured by planktonic algal chlorophyll, water clarity, hypolimnetic oxygen depletion rate, macrophyte growth, better water supply water quality, etc., but have a limited or detrimental effect on fisheries by removing habitat, nursery areas, and decreasing food supply. Tools are being developed to quantify the impact of various eutrophication control measures on fisheries. It is necessary that consideration be given to this beneficial use of waterbodies as well when developing a eutrophication control program for a waterbody. The 314 A activities should in general be expanded to include consideration of the impact of nutrients-eutrophication on fisheries.

The OECD eutrophication study program results provide a technically valid basis for determining the trophic status of a particular waterbody and estimating the water quality benefits that will be derived by controlling the phosphorus load to the waterbody. This approach should become the basis for all 314 A activities. All 314 A studies should include collection of information which would further refine the P load-fish yield relationship shown in Figure 2, with particular emphasis given to refining the P load to each waterbody which causes a significant shift in the quality of fish.

RECOMMENDED POLICY

Increasing the fertility of a waterbody will generally increase overall fish yield. Accompanying this increased yield is a change in the quality of fish to those species which are generally less desirable to the North American culture. One of the most dramatic effects of this type is the loss of cold water fish associated with deoxygenation of the colder hypolimnetic waters. Eutrophication is both beneficial and detrimental to fisheries. It is recommended that the American Fisheries Society develop a policy which would minimize fertility of waterbodies to the maximum extent possible. It is further recommended that research be conducted on the relationship between the degree of fertility of a waterbody and the quality of fish present. Particular attention should be given to the effects of planktonic algal growth on the production of excessive crops of rough fish and stunted fish. As these relationships become better understood, the American Fisheries Society may change its recommendation on minimum P and other nutrient loads in order to maximize yield of more desirable fish types while at the same time minimizing detrimental impact on other beneficial uses of the waterbody.

ACKNOWLEDGMENTS

Support for preparation of this review was provided by the Department of Civil Engineering, Colorado State University, and EnviroQual Consultants & Laboratories, Inc., both of Fort Collins, Colorado. Additional support was provided

by the U.S. State Department Joint Spanish-U.S. Committee for Scientific and Technological Cooperation Contract between the Centro de Estudios Hidrograficos-Ministry of Public Works-Madrid and Colorado State University.

REFERENCES

Conway, C. J. Oxygen Depletion in the Hypolimnion, MS Thesis, University of Wisconsin-Madison, Madison, WI (1972).

Frey, D. G. "Distributional Ecology of the Cisco in Indiana," Invest. Ind. Lakes-Streams, 4:177-228 (1955).

Jones, R. A. and Lee, G. F. "Evaluation of the Impact of Phosphorus Removal at the Danbury, Connecticut Sewage Treatment Plant on Water Quality in Lake Lillinonah," Environmental Engineering, Colorado State University, Fort Collins, Occasional Paper No. 31, April (1978).

Lee, G. F. "Eutrophication," Transactions of the Northeast Fish and Wildlife Conference, May, 1972, pp 39-60 (1973).

Lee, G. F. "Indicazioni per lo sviluppo di un programma di controllo dell'eutrofizzazione delle acque costiere adriatiche della regione Emilia-Romagna." Proc Emilia-Romagna Conference on Eutrophication of Northwest Near-shore Adraitic Sea, pp 100-107 (1978) (Ital.).

Lee, G. F. and Jones, R. A. "An Approach for the Development of a Eutrophication Control Program for the Emilia-Romagna Coastal Waters of the Adriatic Sea," Environmental Engineering, Colorado State University, Fort Collins, Occasional Paper No. 27, December (1977).

Jones, R. A. and G. F. Lee. "Application of US OECD Eutrophication Study Results to Deep Lakes," Presented at IAWPR Post Conference Seminar PS 3 'Eutrophication of Deep Lakes' Gjovik, Norway, June 19-20, 1978. (To be published in Seminar Proceedings).

Lee, G. F. and Jones, R. A. "Water Quality Characteristics of the U.S. Waters of Lake Ontario During the IFYGL and Modeling Contaminant Load-Water Quality Response Relationships in the Nearshore Waters of the Great Lakes," Contract Report (Project No. 03-6-022-35196) submitted to NOAA, Ann Arbor, MI (1979a).

Lee, G. F. and Jones, R. A. "Application of the OECD Eutrophication Modeling Approach to Estuaries," Presented at International Symposium on Nutrient Enrichment in Estuaries, May (1979b). (To be published in symposium proceedings).

Lee, G. F., Rast, W., and Jones, R. A. "Recent Advances in Assessing Aquatic Plant Nutrient Load-Eutrophication Response for Lakes and Impoundments," Environmental Engineering, Colorado State University, Fort Collins, Occasional Paper No. 14, May (1977).

Lee, G. F., Abdul-Rahman, M., and Meckel, E. "A Study of Eutrophication, Lake Ray Hubbard, Dallas, Texas," Environmental Engineering, Colorado State University, Fort Collins, Occasional Paper No. 15, September (1978a).

Lee, G. F., Jones, R. A., and Meckel, E. "Estimated Impact of the Detergent Phosphate Ban in the State of Indiana on Water Quality of Selected Indiana Lakes," Environmental Engineering, Colorado State University, Fort Collins, Occasional Paper No. 18, October (1978b).

Lee, G. F., Rast, W., and Jones, R. A. "Eutrophication of Waterbodies: Insights for an Age-old Problem," Environ. Sci. & Technol. 12:900-908 (1978c).

Lee, G. F., Rast, W., Jones, R. A., and Ortiz Casas, J. L., "La Eutrofizacion de las Aguas Superficiales: Estudio de un Problema Antiquisimo." Centro de Estudios Hidrograficos-Madrid (1979a). (In Spanish and English).

Lee, G. F., Rast, W., and Jones, R. A. "Use of the OECD Eutrophication Modeling Approach for Assessing Great Lakes' Water Quality," Published as Chapter 6 of: Lee, G. F. and Jones, R. A., 'Water Quality Characteristics of the U.S. Waters of Lake Ontario During the IFYGL and Modeling Contaminant Load-Water Quality Response Relationships in the Nearshore Waters of the Great Lakes,' Report to NOAA, Ann Arbor, MI and as Occasional Paper No. 42, Environmental Engineering Program, Colorado State University, Fort Collins (1979b).

Lee, G. F., Jones, R. A., and Rast, W. "Availability of Phosphorus to Phytoplankton and Its Implications for Phosphorus Management Strategies," Proc. IJC-Cornell University Conference on Phosphorus Management Strategies for the Great Lakes, April (1979c).

Lee, G. F., Jones, R. A., Rast, W. "Evaluation of Nitrogen and Phosphorus Loads to Water Supply Reservoirs," AWWA Quality Control in Reservoirs Committee Report (1979d).

Nambu, S., Kunikane, S., Lee, G. F., Rast, W., and Jones, R. A. "Recent Advances in Assessing Aquatic Plant Nutrient Load-Eutrophication Response for Lakes and Impoundments," The Japanese Journal of Water Pollution Research, I:157-167 (1978). (In Japanese).

Newbry, B. W., Jones, R. A., and Lee, G. F. "Application of the OECD Eutrophication Modeling Approach to Cherokee Reservoir and Other TVA Impoundments," Report to the Tennessee Valley Authority, Chattanooga, TN (1979).

Oglesby, R. T. "Relationships of Fish Yield to Lake Phytoplankton Standing Crop, Production, and Morphoedaphic Factors," Journal of the Fisheries Research Board of Canada, 34:2271-2279 (1977).

Rast, W. and Lee, G. F. "Summary Analysis of the North American (U.S. Portion) OECD Eutrophication Project: Nutrient Loading-Lake Response Relationships and Trophic State Indices." US EPA, EPA-600/3-78-008, Corvallis, OR, 454 pp (1978).

Rast, W., Lee, G. F., and Jones, R. A. "Predictive Capability of OECD Eutrophication Study Nutrient Load-Eutrophication Response Model." In press (1979).

Thingvold, D. A. and Lee, G. F. "Persistence of 3-trifluoromethyl-4-nitrophenol (TFM) in Aquatic Environments." In press (1979).

Vollenweider, R. A. "Scientific Fundamentals of the Eutrophication of Lakes and Flowing Waters with Particular Reference to Nitrogen and Phosphorus as Factors in Eutrophication." Technical Report DAS/CSI/68, OECD, Paris (1968).

Vollenweider, R. A. "Advances in Defining Critical Loading Levels for Phosphorus in Lake Eutrophication," Mem. Ist. Ital. Idrobiol. 33:53-83 (1976).

Vollenweider, R. A. "Das Nährstoffbelastungs-konzept als Grundlage für den externen Eingriff in den EutrophierungsprozeB stehender Gewässer und Talsperren, Symposium des Wahnbachtalsperrenver-bandes Veröffentlichung der Vorträge," Z. F. Wasser - und Abwasser-Forschung, 12, Jahrgang Nr2/79 (1979a).

Vollenweider. R. A. Canada Centre for Inland Waters, Burlington, Ontario, Personal Communication to G. Fred Lee, Environmental Engineering, Colorado State University, Fort Collins, CO (1979b).

Welch, J. "The Impact of Inorganic Phosphates in the Environment," US EPA Office of Toxic Substances, EPA 560/1-78-003, Washington, D.C. (1978).

to Bob Behnke with compliments,
Kurt Fausch
[1983]

Profitable stream positions for salmonids: relating specific growth rate to net energy gain[1,2]

KURT D. FAUSCH[3]

Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, U.S.A. 48824

Received November 17, 1983

FAUSCH, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**: 441–451.

A model is developed to predict potential net energy gain for salmonids in streams from characteristics of water velocity and invertebrate drift. Potential net energy gain, or potential profit, is calculated for individuals of three species of juvenile salmonids in a laboratory stream aquarium, based on the energy available from drift minus the cost of swimming to maintain position. The Michaelis–Menten or Monod model is used to describe the relationship between potential profit and specific growth rate. Potential profit was a better predictor of specific growth rate for coho salmon (*Oncorhynchus kisutch*) than for brook trout (*Salvelinus fontinalis*) or brown trout (*Salmo trutta*). Coho salmon always achieved higher specific growth rates than either brook trout or brown trout in concurrent experiments, and maintained growth to lower resource thresholds. In each experiment, fish established intraspecific hierarchies and dominant fish held positions affording maximum potential profit. The use of potential profit as an optimal foraging model was tested by predicting the potential for net energy gain at coho salmon positions from the overall pattern of flow and invertebrate drift in the stream aquarium, and ranking these positions from highest to lowest potential profit. This predicted ranking was nearly identical to the rank observed in the linear dominance hierarchy. The results of experiments confirm ideas of other investigators about mechanisms of microhabitat selection by stream salmonids.

FAUSCH, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**: 441–451.

Le modèle proposé ici permet de prédire les gains énergétiques nets potentiels chez des salmonidés d'eau courante à partir des caractéristiques de la vitesse du courant et de la dérive des invertébrés. Le gain énergétique net potentiel, ou profit potentiel, est calculé chez des individus de trois espèces de saumons immatures dans un aquarium d'eau courante en laboratoire, et le calcul est basé sur l'énergie disponible dans la dérive moins le coût de la nage sur place. Le modèle de Michaelis–Menten ou celui de Monod servent à décrire la relation entre le profit potentiel et le taux de croissance spécifique. Le profit potentiel a une meilleure valeur prédictive du taux de croissance spécifique chez le saumon argenté (*Oncorhynchus kisutch*) que chez l'omble de fontaine (*Salvelinus fontinalis*) ou la truite brune (*Salmo trutta*). Le saumon argenté avait toujours des taux de croissance spécifique plus élevés que la truite arc-en-ciel ou que la truite brune au cours des expériences parallèles et avait un seuil de croissance plus bas. Dans toutes les expériences, il s'établissait une hiérarchie intraspécifique et les poissons dominants occupaient des positions leur allouant le profit potentiel maximal. La valeur du profit potentiel comme modèle optimal d'utilisation des ressources a été éprouvée en prédisant le potentiel de gain énergétique net aux positions du saumon argenté à partir du pattern général d'écoulement de l'eau et de la dérive des invertébrés dans l'aquarium et en mettant les positions par ordre descendant, du plus grand profit potentiel au plus faible. Cet ordre prédit est presque identique à l'ordre observé dans la hiérarchie linéaire de dominance. Les résultats des expériences confirment les hypothèses d'autres chercheurs sur les mécanismes de sélection des microhabitats chez les salmonidés d'eau courante.

[Traduit par le journal]

Introduction

Growth of stream salmonids, as in all fish, is related to net energy gain. To be successful, an organism must maintain a balance between the energy and materials it can get from its environment, and that required for metabolism, growth, and reproduction (Warren 1971). This idea is the major tenet of bioenergetic (Ware 1980) and optimal foraging models (Werner and Mittelbach 1981).

For a stream salmonid, this energy balance can be viewed in terms of the position it maintains in the stream. These fish tend to hold relatively fixed positions, or focal points, from which they make short forays to feed on invertebrates drifting nearby (Kalleberg 1958). Drawing on work by Chapman and Bjornn (1969) and Everest and Chapman (1972), Fausch and White (1981) proposed that salmonids should choose focal points in areas of low water velocity to minimize the energy expended on swimming, yet close to swift currents to maximize access to invertebrate drift. Thus, the potential for net energy gain for a stream salmonid at a specific position can be defined in terms of the energy available from invertebrates drifting nearby, minus the metabolic cost of swimming to maintain position. Additional energy may be required to defend social rank or territory. In terms of foraging theory, optimal stream positions for salmonids are those that maximize the rate of net energy gain.

The potential for net energy gain, hereafter called potential profit, available at positions maintained by stream salmonids should be related to specific growth rate of the fish in a predictable way. Recent efforts to define growth of algal (King 1980) and diatom (Tilman 1981) populations as a function of available resources, and to describe growth of individual fish as a function of rations (Brett 1979), indicate that the relationship between specific growth rate and resources is hyperbolic in both cases and fixed by two important points: the resource threshold or maintenance level at which no growth occurs, and the maximum specific growth rate expressed at high resource levels. Thus, fish holding optimal stream positions that afford maximum net energy gain should also grow at maximum specific rates.

---

[1] Based on a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at Michigan State University.

[2] Michigan Agricultural Experiment Station journal article No. 10518.

[3] Present address: Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO, U.S.A. 80523.

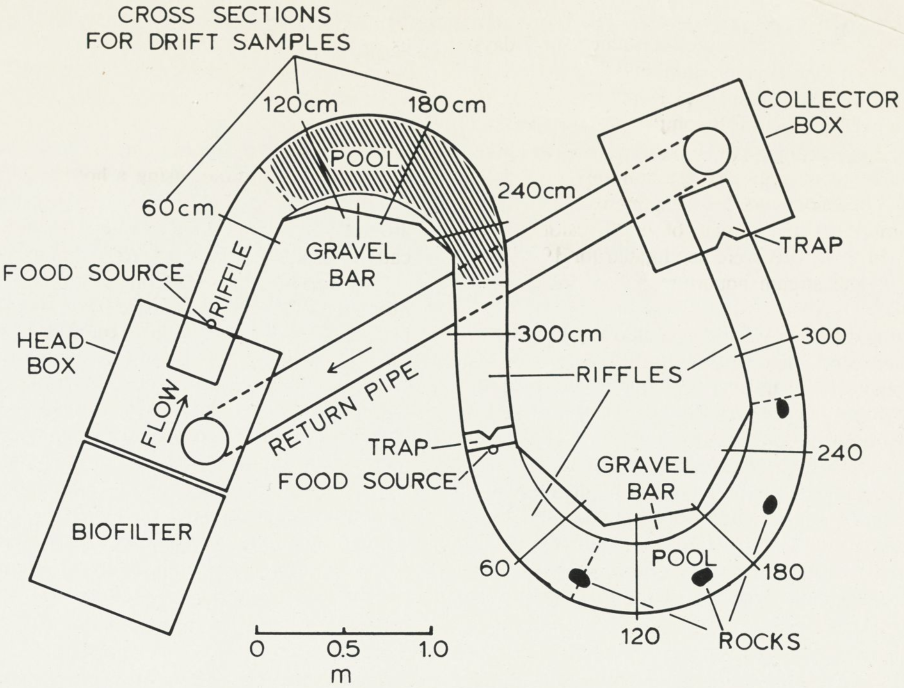


FIG. 1. Plan view of the stream aquarium (after Fausch and White 1983). See text for description of channel features. Water is pumped between head box and biofilter.

The purposes of this paper are first, to define a model of potential profit for positions of stream salmonids in terms of water velocity and drift characteristics that are measurable in streams; and second, to relate the specific growth rates of juveniles of three salmonids, coho salmon (*Oncorhynchus kisutch*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*), to potential profits measured at stream positions of individual fish over 9- to 18-day periods in a laboratory stream aquarium. The results of six experiments show that potential profit was a better predictor of specific growth rate for coho salmon than for brook or brown trout, and provide a test of potential profit as a measure of optimal positions.

Methods

Stream aquarium

Experiments were conducted in a recirculating stream aquarium (Fig. 1) described in Fausch and White (1983). The stream channel was constructed in two sine-generated curves, the pattern of meandering carved by natural streams (Leopold and Langbein 1966). This channel form allowed simulation of natural riffles and pools in the stream bed and provided the diversity of depths and flow characteristics of lotic habitats that are important to juvenile salmonids.

The clear Plexiglas channel shell was 7.28 m long, 30 cm wide, 30 cm deep, and had no slope. It was divided into two 3.64-m sections, each with a V-shaped trap for retaining migrants at its downstream end. The stream bed was formed of 2−3 cm diameter gravel. Pools were 15 cm maximum depth and riffles were 5 cm deep. During each experiment, flow was adjusted according to the swimming ability of the fish to prevent them from all occupying the upstream riffle. Current velocities averaged 20−30 $\mathrm{cm \cdot s^{-1}}$ over riffles and ranged from nearly 0 to 20 $\mathrm{cm \cdot s^{-1}}$ in pools. Four larger rocks were spaced along each section to provide flow refuges for fish (Fig. 1).

All experiments were conducted at 15 ± 0.5°C. Because stream flow was produced by air-lift pumping (cf. Fausch and White 1983), dissolved oxygen was 100% of saturation throughout the stream. Chemical characteristics of the water were maintained at optimum levels by circulating water through a biofilter, built according to Spotte (1979). Ranges, in parts per million (except for pH), for chemical constituents measured at the beginning and end of each experiment were as follows: $\mathrm{CaCO_3}$ alkalinity, 100−128; pH, 8.08−8.53; hardness, 120−140; $\mathrm{NH_3}$-nitrogen, 0.01−0.02; $\mathrm{NO_3}$-nitrogen, 1.83−4.44.

The stream was lit by mercury-vapor and incandescent lamps, the latter brightened and dimmed for 30 min at the beginning and end of the 12-h photoperiod. Light intensity at the water surface varied from 25 to 55 $\mathrm{\mu E \cdot m^{-2} \cdot s^{-1}}$, but was 40 to 55 $\mathrm{\mu E \cdot m^{-2} \cdot s^{-1}}$ for 90% of the stream area. Fish did not prefer areas of low light intensity. Curtains enclosed the stream channel to conceal the observer, who could watch fish through adjustable horizontal slits spaced 40−45 cm along the channel.

Acclimation and experimental design

Six experiments were conducted (Table 1), three with coho salmon, two with brown trout, and one with brook trout. Experiments were run concurrently using different species in each half (1.092 $\mathrm{m^2}$) of the stream aquarium. I used groups of 13−22 fish (12−20 $\mathrm{fish \cdot m^{-2}}$) averaging 33.7−54.1 mm fork length (FL) and 0.26−1.59 g when experiments began (Table 1). Fish were selected to be as uniform in length as possible.

All brook and brown trout were hatched from eggs of wild trout from Michigan streams, and coho salmon from eggs of returning Lake Michigan fish. After hatching, larvae were transferred to gravel beds in a stream holding tank and isolated from disturbance to promote normal development and emergence. At the swim-up stage, fry were fed frozen *Daphnia*, later supplemented with commercial trout feed and *Artemia*. Fish were maintained on a 12-h photoperiod and were gradually acclimated to 15°C at least 1 week prior to the start of each experiment.

During each experiment, invertebrate drift was simulated with *Daphnia* introduced continuously in the riffle at the head of each section throughout the light cycle. Although a point source of food could potentially be defended by one dominant fish, small size of *Daphnia* and relatively high velocities, especially on the riffles, ensured that no one fish could capture the majority of drift particles. Prior to experiments, fish were acclimated to the stream aquarium and feeding on drifting *Daphnia* for periods ranging from 4 to 25.5 days (Table 1). During experiments 1 and 2, fish were acclimated to both food and the stream aquarium for 4 days before the 18-day experiments. During experiments 3 and 4, fish were acclimated for 7 days to the food, the last 5 days to the stream aquarium, and then grown for 10.5 days together in sympatry (10 coho and brook trout in each stream half) as part of an experiment to test competition between the two species, to be reported in another paper. Fish were then weighed, measured, and isolated in allopatry in the downstream traps for 2 days under low light and flow conditions and fed a maintenance ration, a procedure designed to minimize the effects of prior residence on subsequent experiments. In total, fish were acclimated for 19.5 days to food and 17.5 days to the stream aquarium before the 10-day experiments.

Prior to experiments 5 and 6, fish were acclimated for 14 days to both stream aquarium and food, then grown for 9.5 days in sympatry and isolated for 2 days in the traps for a total of 25.5 days of acclimation prior to the 9-day experiments. The acclimation period appeared critical, especially for the trout, and was increased throughout experiments. Fish appeared acclimated to light and flow conditions in the stream aquarium after about 4 days, but physiological acclimation to feeding on drifting *Daphnia* probably took much longer.

To determine suitable fish density, coho salmon and brown trout could migrate out of the sections into downstream traps during experiments 1 and 2. Migrants were returned to the head of the section three times before removal from the experiment. Of the original 25 fish of each species, 17 brown trout and 22 coho salmon remained in the channel. In all other experiments, traps were blocked to prevent fish from leaving the channel to maintain equal densities for tests of interspecific competition described above.

Fish in each experiment were individually marked prior to acclimation by excising fin tips in combinations of no more than four of the following five fins: dorsal (D), anal (A), adipose (X), top caudal lobe (T), and bottom caudal lobe (B). Most fish were given one to three fin clips, which did not appear to affect normal behavioral displays. There was no difference in growth rates of fish receiving one, two, or three fin clips by a Kruskal–Wallis test ($p > 0.30$ or greater for all experiments).

Fish were measured (FL because of fin clips) and weighed at the beginning and end of each experiment after being starved for 12 h (2000–0800 eastern daylight time (EDT)) to reach a standard level of gastric evacuation. Fish were individually anesthetized (tricaine methanesulfonate, MS 222), measured (±0.25 mm), blotted lightly on a cloth towel, and weighed (±0.005 g) in a beaker of water tared on a balance. Specific growth rates (μ, days^{-1}) for each fish were calculated from

$$[1] \quad \mu = \frac{\ln W_t - \ln W_o}{t}$$

where W_t is the final weight (grams), W_o is the initial weight (grams), and t is the growth period to the nearest 0.5 days.

Invertebrate drift

The frozen *Daphnia* introduced at the upstream end of each section to simulate drifting invertebrates were thawed in a carboy of stream aquarium water and mixed with minimal air-stone bubbling. The mixture required 3 h to drain through a small orifice so the carboy was refilled four times daily. Random samples of frozen *Daphnia* were dried (24 h at 105°C), ashed (3 h at 550°C), and weighed (Table 1). Mean percent ash was 8.26 (SE, 0.373) for all experiments.

During experiments 3–6, drift was measured at five cross sections located at 60-cm intervals along each section (Fig. 1) using 0.3-mm mesh nets measuring 5 × 5 cm at the mouth with 18 cm long bags. Nets were fixed to frames that rested across the top of the channel wall, which were placed through narrow openings in the curtain to minimize disturbance to fish. During 20-min drift samples at each cross section, two nets were positioned at least 5 cm apart to prevent flow disturbance of one net from affecting the other. Nets were fished at only one cross section at a time, and drift at each cross section was sampled eight times in each experiment. During experiments 1 and 2, drift was sampled at only three cross sections (60, 180, and 300 cm) using four or five nets per cross section for 120-min periods. In all experiments, fish became conditioned to disturbance of drift sampling and returned to normal positions soon after drift nets were positioned.

After drift samples, I removed the nets and measured water velocities at points corresponding to the center and edges of each net along its horizontal midline, using a hot-bead anemometer modified from LaBarbera and Vogel (1976). Water-velocity profiles measured around net frames with and without nets showed that the netting caused an 8.6% (SE, 2.18) reduction in velocity on average.

Daphnia were washed from drift nets and counted under 15× magnification. The drift consisted of a mixture of sizes of whole and broken *Daphnia*, and during experiments 1 and 2 fish were observed to select those items larger than about 0.5 mm. Owing to this size selectivity, I counted only *Daphnia* larger than 0.5 mm during experiments 3–6. In all experiments I set the largest *Daphnia*, which were about 2 mm, as the standard unit and equated three smaller whole or partial ones to one standard 2-mm *Daphnia*.

Because some *Daphnia* were broken I suspected that thawing, mixing, and drifting them in water may have ruptured their bodies and reduced their caloric content to fish. To convert drift counts to caloric value, I first counted and dried (24 h at 105°C) 10 samples of *Daphnia* thawed in stream water, mixed for 1.5 h (mean residence time in carboy) with an air-stone to simulate carboy treatment, and strained in a drift net. These samples averaged 117×10^3 standard 2-mm *Daphnia* per gram dry weight (SE, 5.4×10^3). Similarly, to convert dry weight to calories I circulated, strained, dried, and combusted five replicates in a bomb calorimeter. Standard *Daphnia* yielded 5938 cal·g dry weight^{-1} (SE, 19.6) (1 cal = 4.1868 J), which is close to values reported by Cummins and Wuycheck (1971) and indicates that treatment of *Daphnia* did not reduce their caloric content. Combining these data, a fish would have to capture 19.7 standard *Daphnia* from the drift to gain 1 cal.

Potential profit at fish positions

I estimated the potential profit for each fish each day based on a measure of *Daphnia* drifting within the feeding range of a fish's position, minus the cost of swimming to maintain position. Thus,

$$[2] \quad P = D - S$$

where P is the potential profit (calories per hour), D is the available drift energy (calories per hour), and S is the swimming cost (calories per hour). During all experiments, most fish maintained the same position for many days, so I assumed that a daily measurement of their position was adequate to estimate potential profit exclusive of energy required for agonism.

The cost of swimming (S) was calculated from the focal-point water velocity measured at the fish's head, using the general metabolic equations Stewart (1980) developed for coho salmon and rainbow trout from a review of literature on swimming metabolism of salmonids. This estimate excluded the energy required for short forays to capture drifting food. I transformed Stewart's (1980) equations to calculate swimming cost (calories per hour) at 15°C given fish weight and water velocity.

$$[3] \quad \text{Coho salmon: } S = 0.9906W^{0.784}\mathrm{e}^{0.0186V}$$

$$[4] \quad \text{Rainbow trout: } S = 0.7007W^{0.763}\mathrm{e}^{0.0327V}$$

where W is the fish weight (grams) and V is the focal-point water velocity (centimetres per second).

To estimate the drift available to fish (D), I needed to determine (*i*) the average foraging distance from their focal points, (*ii*) the rate at which drift energy passed through the foraging area, and (*iii*) the portion of drift energy available to each fish. During a pilot study, coho salmon and brown trout were observed to forage to a distance of about two body lengths (FL), mainly in the area of maximum velocity within the quarter sphere above and in front of their focal point. In further tests, I placed a ruler beneath the foraging area of two different coho salmon positioned in pools, and measured only horizontal forays along the ruler. Feeding frequency of these fish dropped off sharply at distances further than two body lengths from the focal point, even though higher water velocities delivered more food per unit time at some points there. I also observed that many fish chose positions in pools about two body lengths from the stream wall. Wankowski (1981) found that the area of capture upstream of positions held by juvenile Atlantic salmon (*Salmo salar*) was fan-shaped in the horizontal plane, and that capture distance varied seasonally from 1.9 to 9.9 body lengths. Although the area of drift capture for stream salmonids should be expected to vary with water velocity, particle size and abundance, hunger level, and species, it appears that my "two body length" criterion may be a conservative estimate for the foraging distance of juvenile salmonids.

To determine the rate at which drift passed through the foraging radius, I used drift-sample results presented below to map drift rates as a function of water velocity throughout the channel for each experiment. The amount of drifting *Daphnia* decreased downstream owing to predation and sinking. Juvenile salmonids captured only moving particles, ignoring those that sank into interstices in the stream bed.

The final problem was to determine the portion of drift passing through the foraging area that was available to fish. Because fish foraged mainly in about one-quarter of their semicircular feeding radius where the maximum velocity and highest drift rate occurred ($1/8\pi r^2$ envisioned in the vertical plane with the focal point at the center of the circle), I assigned each fish the drift energy passing through this pie-shaped "window" at a rate dictated by the maximum velocity measured within the two body length radius above and in front of the focal point. Thus,

$$[5] \quad D = 1/8\pi r^2 \cdot E$$

where r is the two body length feeding radius (centimetres) and E is the drift energy rate at maximum velocity (calories per hour per square centimetre). Relationships for E are developed below as functions of water velocity and distance from the upstream food source. The mean FL of fish when each experiment began was used to calculate feeding radius.

In summary, calculating potential profit at fish positions using this model requires measuring drift energy rate and three position characteristics: focal-point velocity, maximum velocity within the feeding radius, and distance of position from the upstream end of the section. Water velocities were measured either with midget Bentzel speed tubes (Everest 1967) (range, $3-30\ \mathrm{cm \cdot s^{-1}}$) or with the hot-bead anemometer (range, $0.1-3.0\ \mathrm{cm \cdot s^{-1}}$), and distances were measured from a scale along the stream wall.

Half of the fish in each experiment were chosen randomly for position measurements during morning or afternoon each day. To minimize disturbance, all fish positions to be measured were first marked on the Plexiglas stream wall with wax pencil and the stone directly beneath them on the stream bed recorded. Curtains then were opened and characteristics of each position measured. Drift was measured in random order from 1100 to 1300 EDT each day and fish positions were measured at other times between 0800 and 01800 EDT.

The relationships between specific growth rate of individual fish and potential profit were fitted to Michaelis–Menten or Monod functions of the form

$$[6] \quad \mu = \mu_{\max} \frac{(P - T)}{(K_{\mathrm{P}} - T) + (P - T)}$$

where $\mu_{\max}$ is the maximum specific growth rate ($\mathrm{day^{-1}}$), K_{P} is the resource level at $1/2\ \mu_{\max}$ (half-saturation constant in calories per hour), and T is the resource threshold at which no growth occurs (calories per hour). If the resource threshold is zero, the equation simplifies to the original Michaelis–Menten form which passes through the origin. In practice, I first estimated the threshold (T) using points close to the x-axis, then subtracted this threshold value from all data to transform the equation to the simple form and used the best fit of three reciprocal plots outlined in Dowd and Riggs (1965) to determine the equation.

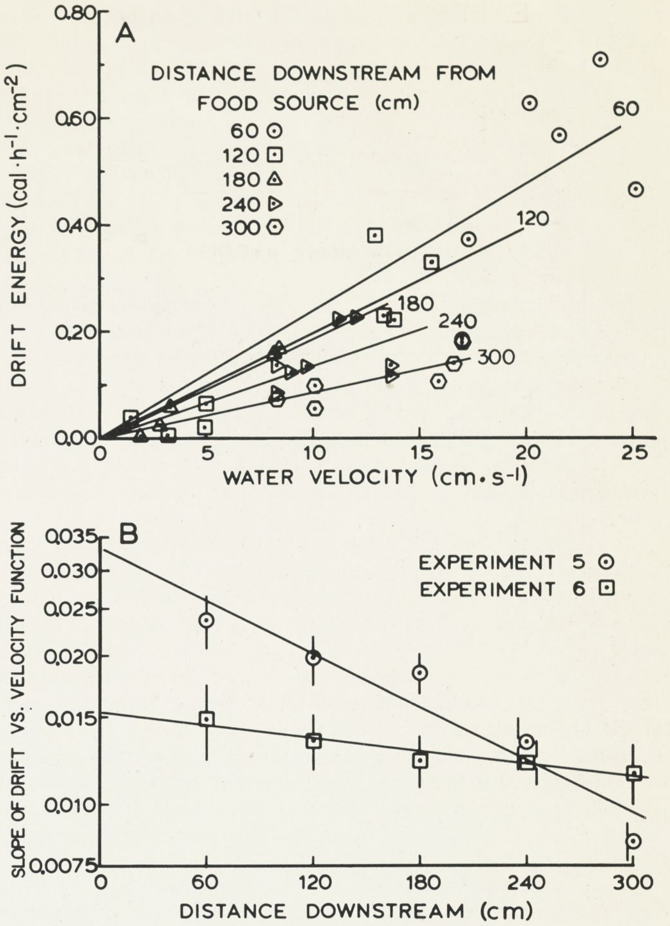


FIG. 2. (A) Drift energy as a function of water velocity at five distances from the upstream end of the stream aquarium during experiment 5. (B) Slope of the drift vs. velocity relationship (±SE) as a function of distance from the upstream end during experiments 5 and 6.

Results

Drift energy

In all experiments, the energy available to fish as drift was a linear function of water velocity for each of the five cross sections (Fig. 2A) so that

$$[7] \quad E = m \cdot V$$

where E is the drift energy (calories per hour per square centimetre) and m is the slope of the drift vs. velocity relationship. These linear relationships were often better for the three pool cross sections (120, 180, and 240 cm in Fig. 1) than for the 60- and 300-cm cross sections in the riffles. At the 60-cm distance the drifting *Daphnia* were not evenly distributed across the channel in proportion to flow despite a small baffle positioned just downstream of the food input for this purpose. The best drift vs. velocity relationships were achieved during experiments 5 (Fig. 2A) and 6 when the sampling and counting techniques were most refined. All linear regressions were significant for all experiments ($p \leq 0.01$), but because they were forced through the origin conventional coefficients of determination (r^2) could not be calculated.

The decline in slopes of drift vs. velocity relationships with distance downstream from the food source was fitted to a negative exponential equation (Fig. 2B),

$$[8] \quad m = ae^{-bx}$$

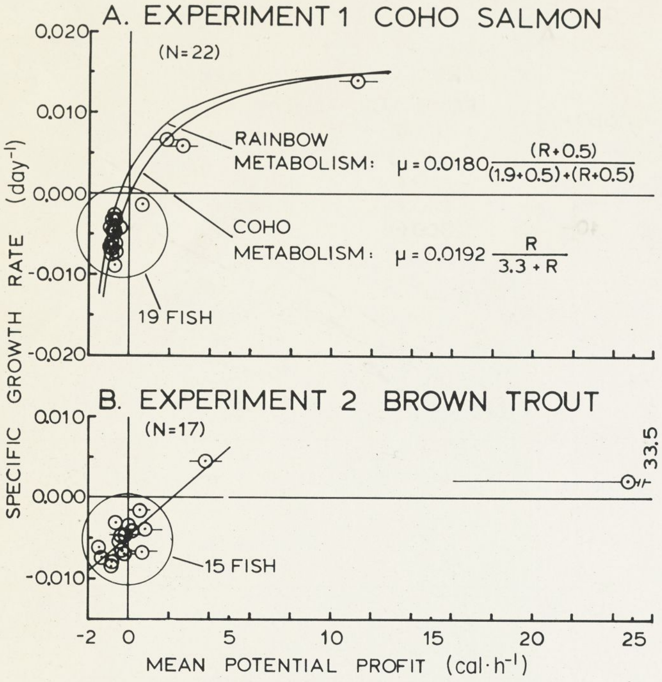


FIG. 3. Specific growth rates of (A) coho salmon (experiment 1) and (B) brown trout (experiment 2) as a function of mean potential profit. Points in (A) are for coho metabolism only (see text). Horizontal lines show 95% confidence intervals where greater than 1.0 cal$\cdot$h^{-1}.

where x is the distance downstream from food source (centimetres) and a and b are constants. To determine the available drift energy (D) at a fish's position, Eq. 8 may be substituted into Eq. 7, and the result substituted into Eq. 5, yielding

$$[9] \quad E = ae^{-bx} \cdot V$$

$$[10] \quad D = 1/8\pi r^2 \cdot ae^{-bx} \cdot V$$

so that the available drift energy is a function of fish body length ($1/2r$), distance downstream from the food source (x), and water velocity (V), the last being the maximum velocity within the two body length radius. Drift equations (Eq. 8) for each experiment are presented in Table 1.

Specific growth rate vs. potential profit

In experiments 1 and 2, few fish grew because food levels were low (Fig. 3). Despite this constraint, the specific growth rates of coho salmon were a hyperbolic function of mean potential profit at their stream positions, which fit the Michaelis–Menten model well. Of the 22 coho in experiment 1, 19 lost weight and 18 of these held positions requiring a net energy expenditure as shown by the negative mean potential profit. The 95% confidence intervals for mean potential profit are shown in Fig. 3 and subsequent figures, but only for fish with confidence intervals of 1.0 cal$\cdot$h^{-1} or greater. The narrow confidence intervals in Figs. 3A and 3B indicate that coho salmon and brown trout often used the same positions or ones with similar characteristics throughout the 18-day experiments.

There was little difference in Michaelis–Menten curves whether swimming cost was calculated using equations for coho salmon (Eq. 3) or rainbow trout (Eq. 4) (Fig. 3A). In subsequent experiments, the coho metabolic equation was used to calculate swimming costs for coho, and the rainbow trout equation was used for brook and brown trout. The resource threshold at which no growth occurred for coho salmon in experiment 1 (T in Eq. 6) was 0.0 cal$\cdot$h^{-1} for coho metabolism and -0.5 cal$\cdot$h^{-1} for rainbow metabolism, although the latter is theoretically impossible. Moreover, since mean potential profit did not include additional energy costs such as metabolism at night and aggressive displays, true resource thresholds may be slightly lower than calculated. Resource thresholds should vary slightly with changes in fish size and drift measurement, so results are most comparable between experiments run concurrently because fish size, acclimation, food level, and drift measurement are nearly identical.

The data for brown trout from experiment 2 (Fig. 3B) are not adequate to fit the Michaelis–Menten model, but the resource threshold was estimated to be approximately 2.1 cal$\cdot$h^{-1} by linear regression. Of the 17 fish that remained in the experiment, only 2 grew, and 1 of these was excluded *a priori* because its position was characterized by highly variable potential profits indicated by the large confidence interval in Fig. 3B. This fish held a focal point in a crevice on the upper riffle for most of the experiment, but was able to capture only a small proportion of the drift passing by owing to the high water velocities overhead, and was therefore not able to garner the same proportion of potential profit that other fish did.

In all experiments, individual fish occasionally swam to other parts of the stream for short periods and used atypical positions. If these positions had abnormally high or low potential profit values relative to other days, they were statistically excluded as outliers by the method of Grubbs and Beck (1972). Mean potential profit was then recalculated using the remaining measurements.

The behavior of juvenile brook and brown trout with regard to holding positions tended to differ from coho salmon in two ways. First, brown trout forced into positions in fast water often applied the leading edges of their pectoral fins to the stream bed to hold themselves on the bottom with little energy expenditure. Brook trout also did this occasionally, and Gibson (1981) and Kalleberg (1958) have reported that Atlantic salmon also use this technique. Coho salmon never rested on the bottom. Whenever trout were observed resting on the bottom in experiments 2 and 4, they were assigned a focal-point velocity and maximum velocity of 0.0 cm$\cdot$s^{-1}, because they seldom appeared to forage and I assumed they required only their standard metabolic rate to maintain position. I modified my technique during experiment 6, and assigned brown trout a focal-point velocity of 0.0 cm$\cdot$s^{-1} and a maximum velocity measured only to the small distance from their focal point that they were observed to travel to capture drift.

A second distinguishing characteristic of trout was that subordinate fish tended to hide in the gravel, often lodging themselves next to the Plexiglas stream wall. These fish were also assigned focal-point and maximum velocities of 0.0 cm$\cdot$s^{-1}.

In experiment 3, coho salmon grew at much higher rates than in experiment 1, and only two fish lost weight (Fig. 4A), probably because fish were acclimated longer and fed more than the previous experiment (Table 1). The Michaelis–Menten function was difficult to fit to these data because no fish grew near the maximum specific growth rate, but the resource threshold required for maintenance was estimated to be 2.5 cal$\cdot$h^{-1}. As in experiment 1, coho positions showed little variability in mean potential profit, as indicated by the small 95% confidence intervals in Fig. 4A. One coho salmon disappeared into the gravel on the last day of the experiment and was never found.

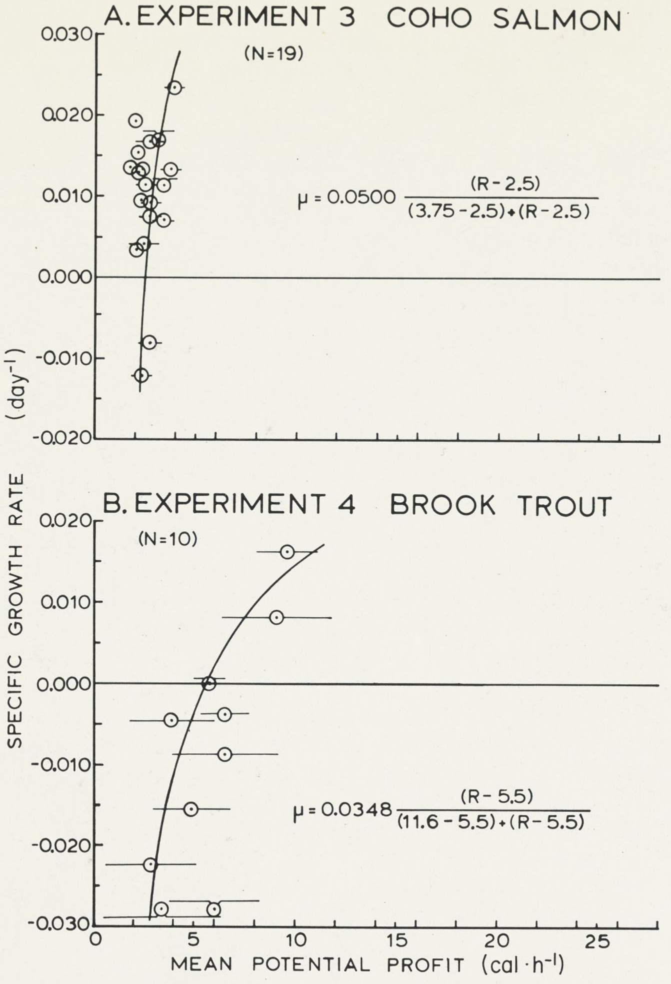


FIG. 4. Specific growth rates of (A) coho salmon (experiment 3) and (B) brook trout (experiment 4) as a function of mean potential profit. Horizontal lines show 95% confidence intervals where greater than 1.0 cal $\cdot$ h^{-1}.

In contrast, only three brook trout grew or maintained their weight in experiment 4 when fed at the same rate as coho salmon were in experiment 3 (Fig. 4B). Brook trout grew at a lower specific rate for a given mean potential profit, required a higher resource threshold to maintain their weight (5.5 cal $\cdot$ h^{-1}), and occupied positions with more variable mean potential profit than did coho salmon. Experiment 4 was begun with 20 brook trout, but 2 fish died by the 4th day of the experiment and 8 fish burrowed into the gravel at the downstream end of the section and were never recovered. All these fish were healthy, but all held unfavorable positions with negative mean potential profits for the days before they disappeared indicating that they were probably losing weight rapidly

In experiment 5, coho salmon grew similarly to those in experiment 3 and several fish had high specific growth rates, providing the most complete data set of any experiment for fitting the Michaelis–Menten function (Fig. 5A). All coho salmon grew, although the 95% confidence intervals indicate that some fish held positions with more variable potential profit than during experiments 1 and 3. One coho salmon held a position in a crevice on the upper riffle and was excluded *a priori* for the same reasons that a brown trout using a similar position was excluded in experiment 2. The resource threshold for coho salmon during this experiment was 1.1 cal $\cdot$ h^{-1}.

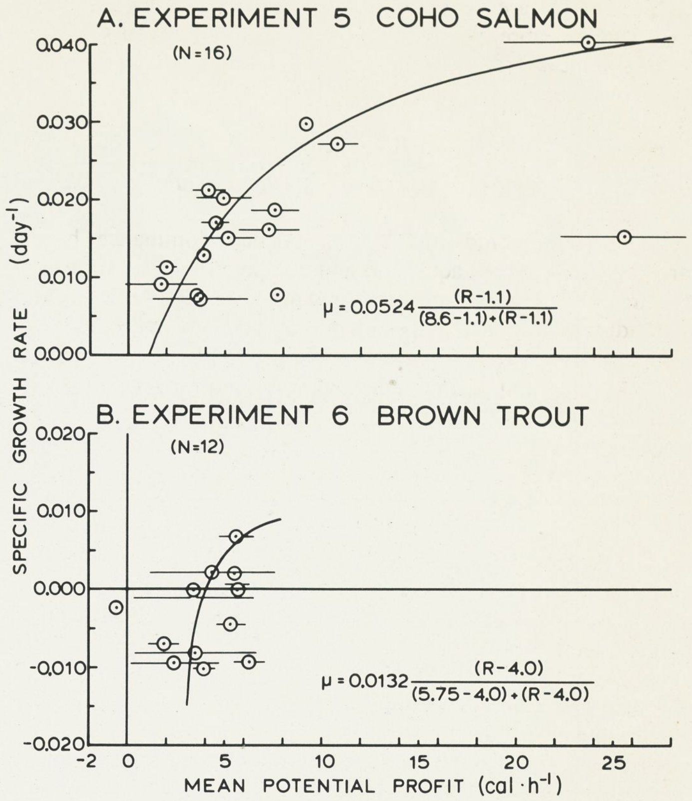


FIG. 5. Specific growth rates of (A) coho salmon (experiment 5) and (B) brown trout (experiment 6) as a function of mean potential profit. Horizontal lines show 95% confidence intervals where greater than 1.0 cal $\cdot$ h^{-1}.

Only five brown trout in experiment 6 grew or maintained their weight when fed at the same level as coho salmon in experiment 5 (Fig. 5B). Brown trout grew at lower specific rates than coho at all levels of potential profit, required a higher resource threshold to maintain growth (4.0 cal $\cdot$ h^{-1}), and often held positions with more variable potential profits than coho did. This pattern is similar to that when brook trout and coho salmon in experiments 3 and 4 are compared (Figs. 4A and 4B). One fish that hid in the gravel throughout the experiment was not recovered.

The ranking of fish in linear dominance hierarchies was known owing to continuous observation of the fish throughout each experiment. This ranking generally agreed with the order of fish along the specific growth rate vs. potential profit curve. That is, the dominant or highest ranking individual defended an area with the highest resource level, and the hierarchy of subordinates held positions affording successively lower potential profits. This behavior produced the patterns seen in all experiments, especially experiments 1, 2, and 5, where one individual far exceeded others in mean potential profit and specific growth rate. This pattern produced by the dominance hierarchy makes fitting the Michaelis–Menten equation using reciprocal plots difficult, because the variability inherent in measuring small potential profits and growth rates of the most subordinate fish (corresponding to points close to the threshold) is magnified when the reciprocal is calculated, and exerts a strong influence on the linear regression used to fit the equation (see Methods). Moreover, this variability makes the coefficients of determination (r^2) for reciprocal plots of little use as a goodness of fit measure for these Michaelis–Menten functions. Thus, these functions are easier to fit if more fish grow at higher rates and data are more evenly spaced. For example, even spacing can be achieved in aquaculture research when individual fish are grown separately on known rations.

Discussion

Specific growth rate vs. resources: the Michaelis–Menten model

Juvenile salmonids quickly established dominance hierarchies in the stream aquarium and competed for a position in the area of stream that afforded maximum potential profit. The individual fish in each experiment that held this optimal position also showed the highest specific growth rate.

Mean potential profit generally was a better predictor of specific growth rate, using the Michaelis–Menten model, for coho salmon than for either brook or brown trout. The variability inherent in all the specific growth rate vs. potential profit relationships is attributable to several factors. First, the time required for physiological and behavioral acclimation of fish to the food and stream aquarium may be longer than allowed, although I increased the initial acclimation period in allopatry from 4 to 14 days (see Methods). This is significantly longer acclimation than used during most other studies of stream salmonids. Second, mean potential profit may be biased because drift is difficult to measure accurately, equations for swimming metabolism are available for few species and may not be accurate for small fish, and the energy spent on agonism and forays to catch drift could not be determined. Third, enforced rather than volitional residence may have caused subordinate fish that would have emigrated to grow below their potential given available food, owing to energy wasted on agonism. A fourth possible reason for higher variability in trout relationships is that trout tended to use their pectoral fins to maintain position on the stream bed when swimming costs were high, which may have biased estimates of potential profit.

Despite these constraints the results of these experiments (Figs. 3–5) can be added to the growing body of evidence suggesting that the Michaelis–Menten or Monod equation describes the relationship between specific growth rate and a critical resource for a wide range of organisms. This approach has most often been used to describe population growth of bacteria (Monod 1949), algae (King 1980), and diatoms (Tilman 1981) but more complex organisms show similar relationships. For instance, specific growth rates for populations of two zooplankton species (*Daphnia pulex* and *D. rosea*) grazing on phytoplankton (Lampert and Schober 1980) follow the Michaelis–Menten form. Specific growth rates of pelagic juvenile sockeye salmon (*Oncorhynchus nerka*) as a function of zooplankton density in British Columbia lakes (Brocksen et al. 1970) also appear to fit the Michaelis–Menten function, but in neither of these studies were equations fitted.

It is important to distinguish between specific growth rates of populations as opposed to those for individual organisms. Rates for populations include births, deaths, and costs of reproduction, whereas rates for individuals describe only body growth (cf. Lampert and Schober 1980).

The specific growth rates of fish fed known rations in aquaculture feeding trials (cf. Brett 1979) also may be described by Michaelis–Menten relationships. Stauffer (1973) fitted various functions to data from Brett et al. (1969) but favored a modified sine function over the Michaelis–Menten because it fit the data better. However, further inspection revealed three differences between Stauffer's (1973) methods and mine that affected the resulting equations. First, he ignored fish that were fed to satiation or excess and consequently grew at high specific rates. Fitting the Michaelis–Menten is difficult without points near the maximum specific growth rate (e.g., experiment 3, Fig. 4A). Second, to account for the resource threshold or maintenance ration, Stauffer (1973) transformed the axes to the point on the curve where $P = 0$ (Eq. 6), i.e., a point corresponding to the negative specific growth rate if fish were not fed. This makes fitting the equation difficult because points other than $\mu_{\max}$ and K_P must be estimated, a reason he rejected the equation. Third, Stauffer (1973) estimated $\mu_{\max}$ and K_P by inspection from curves Brett et al. (1969) fitted by eye. My preliminary analyses of these data show that substantially better fits would result if Michaelis–Menten parameters were calculated using reciprocal transformations (Dowd and Riggs 1965) or nonlinear regression (Bliss and James 1966).

Carline and Hall (1973) found hyperbolic relationships for specific growth rates of coho salmon fed known amounts of fly larvae in an artificial stream and aquaria. Quadratic equations they fit show that maximum specific growth rates were 0.012–0.020 $g \cdot g^{-1} \cdot day^{-1}$ for 45- to 78-mm fish, close to the range I observed for fish of similar size. Carline and Hall (1973) and Stauffer (1973) used ingested ration as their measure of resources whereas potential profit measures resource availability. Warren (1971), Stauffer (1973), and Carline and Hall (1973) all suggest that the specific growth rate vs. ration curve falls off at high rations because net growth efficiency decreases linearly above the maintenance ration as a result of decreased assimilation efficiency as more food moves through the gut, increased specific dynamic action, or increased activity. In this study, an additional factor contributing to the hyperbolic nature of the function is that high-ranking fish became satiated at profitable positions after 6–8 h and captured a smaller proportion of drift than subordinate fish at poorer positions.

The model of growth outlined in this paper depends on the fundamental idea that populations and individuals grow exponentially, but that specific growth rate declines as resources are depleted according to the Michaelis–Menten function (Eq. 6). Not considered here are cases where more than one resource is in short supply. Young and King (1980) and Tilman (1981) use this model to describe interacting effects of multiple resource limits on algae and diatoms.

The strengths of the Michaelis–Menten model for describing growth lie in four areas. First, the parameters are biologically meaningful. For individual organisms the resource threshold (T) corresponds to the maintenance ration (R_{maint} of aquaculturists, Brett 1979) and the maximum specific growth rate ($\mu_{\max}$) is a genetically constrained maximum ($r_{\max}$ of ecologists, when referring to populations).

Second, the equation provides clearer insight into the mechanisms of population or individual growth, in contrast to density-dependent models of population growth, such as the Verhulst–Pearl logistic (Kingsland 1982), or the various empirical models of individual fish growth in relation to age, such as the von Bertalanffy model (cf. Ricker 1979). Growth of individuals or populations is related to resources, such as food or space, and should be tractable in this form if critical resources can be measured. Third, the relationship appears to be a general one for organisms. It has thus far been used for organisms ranging from bacteria to fish and should apply to others, requiring only that populations grow exponentially subject to resource constraints.

Finally, these relationships are useful in comparing resource

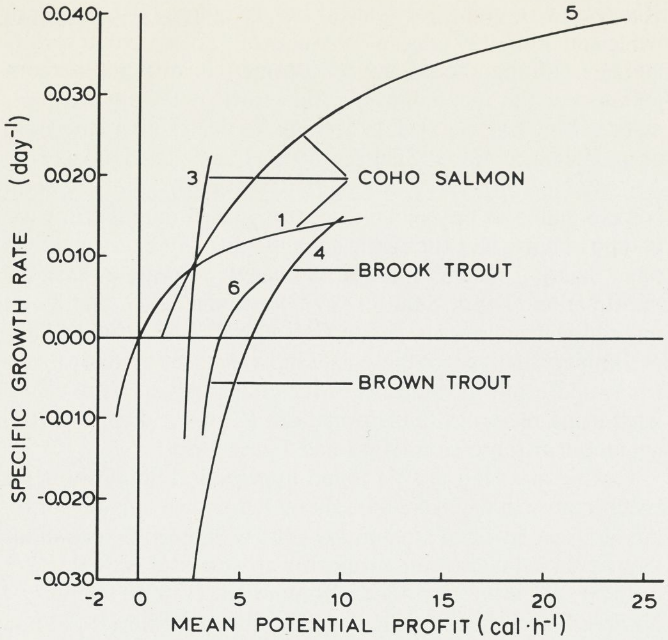


FIG. 6. Specific growth rate vs. mean potential profit curves for all experiments in which Michaelis–Menten equations were fitted. Numbers by curves refer to experiments.

use and predicting competitive ability of different species (Healey 1980; Tilman 1981). Such relationships measured in allopatry can be used to make *a priori* predictions about which species will grow faster in sympatry, and which will maintain growth to lower resource levels. In all experiments, coho salmon maintained growth to lower resource thresholds than either brook or brown trout (Fig. 6) and, except for experiment 1, coho always showed higher specific growth rates than trout for a given resource level. As mentioned above, comparisons of these curves are most appropriate for experiments run simultaneously. These results lead one to predict that coho salmon would grow faster when paired with equal-sized trout of either species in sympatry and would continue growing at lower food levels.

Potential profit as an optimal foraging model

The major assumption of optimal foraging models is that organisms maximizing net energy gain also maximize fitness (Pyke et al. 1977). In this respect the model of potential profit is an optimal foraging construct, based on drift and flow characteristics at feeding positions of stream salmonids. Proponents of the theory argue that the strength of optimal foraging models lies in their ability to predict behavior of an animal given an array of food or habitat resources from which to choose (Werner and Mittelbach 1981). Although variations of these models have proliferated, relatively few have been tested, especially in the field. A rigorous test of an optimal foraging model involves comparing observed resource use of an organism with that predicted by the model from knowledge of the resource distribution in the environment.

This approach has been used successfully by Werner and Hall (1974, 1979), Werner (1977), and Mittelbach (1981) for fish that compete exploitatively, but I modified it to make predictions about microhabitat use or position choice by stream salmonids, which set up linear dominance hierarchies through interference competition (Jenkins 1969). Within the short section of stream aquarium where all fish in an experiment can potentially interact, I hypothesize that fish compete for optimal positions that maximize potential profit. Moreover, because juvenile salmonids defend areas around their focal points, use of a position by one fish precludes use by all others of lower rank in the hierarchy. Therefore, corresponding to the decrease in rank along the linear dominance hierarchy should be a similar hierarchy of positions offering successively less potential profit.

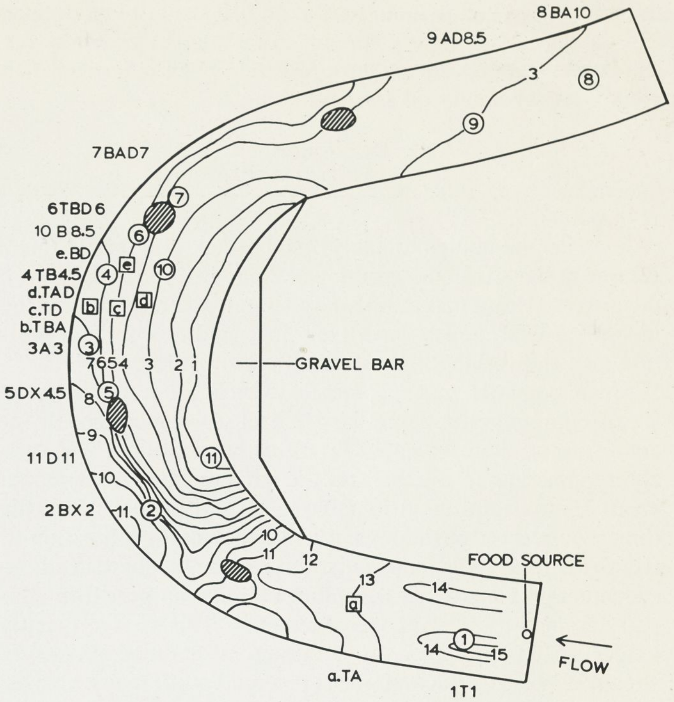


FIG. 7. Map of mean potential profit (calories per hour) at focal points close to the stream bed in the upstream section during experiment 5. Hatched areas are rocks. Circles are fish positions ranked according to the dominance hierarchy, and corresponding letters are fin-clip codes. Numbers preceding the fin-clip codes are observed dominance rank, and numbers following the codes are rank of predicted potential profit. See text for further explanation.

To test this hypothesis I compared positions held by juvenile coho salmon in the upstream half of the stream aquarium during experiment 5 with the pattern of potential profit in this section predicted by the model. To map potential profit, I measured water velocity at identical points for three depths: 2.5, 7.5, and 12.5 cm. At each of 89 points the velocity closest to the stream bed was used as the focal-point velocity, and the maximum velocity within two body lengths (83 mm for coho salmon in experiment 5) above and in front of the focal point was determined from three-dimensional velocity profiles. Using the drift equation for experiment 5 (Table 1) and these velocity characteristics, potential profits for each focal point were determined using Eqs. 2, 3, and 10, and contours of equal profit mapped in Fig. 7.

Typical positions for the coho salmon are also shown (Fig. 7), with letters designating their fin-clip codes. Of the 16 fish positions, 5 shown as squares were atypical in relation to the map and deserve mention. Fish TA on the upper riffle did not grow according to its potential and was excluded for reasons described in Results. Four of the most subordinate fish occupied the lower pool (TBA, TD, TAD, and BD) and usually held positions 7–14 cm above the stream bed. These were not considered because potential profit contours apply only to fish

TABLE 1. Design of experiments and relationships between slopes of drift energy vs. water velocity regressions (m) and distance downstream from the food source (x)

Experiment	Stream section[a]	No. of days		No. of fish	Mean initial		Dry weight (g) *Daphnia* fed per day	Drift equation[b]	r^2[c]	p
		Acclimation	Experiment		Length (mm)	Weight (g)				
(1) Coho salmon	U	4	18	22	54.1 (50.5−57.5)[d]	1.59 (1.21−2.03)	0.280 (0.0124)[e]	$m=0.1002e^{-0.0236x}$	0.99	<0.05
(2) Brown trout	D	4	18	17	52.4 (47.5−54.5)	1.40 (0.99−1.63)	0.172 (0.0172)	$m=0.0546e^{-0.0207x}$	0.99	<0.05
(3) Coho salmon	D	17.5[f]	10	20	35.1 (32.0−38.0)	0.32 (0.20−0.49)	0.314 (0.0090)	$m=0.0246e^{-0.00305x}$	0.84	<0.01
(4) Brook trout	U	17.5[f]	10	18	33.7 (30.0−37.0)	0.26 (0.15−0.45)	0.314 (0.0090)	$m=0.0330e^{-0.000747x}$	0.49[g]	<0.15
(5) Coho salmon	U	25.5	9	16	41.3 (39.0−43.5)	0.62 (0.46−0.87)	0.418 (0.0112)	$m=0.0330e^{-0.00410x}$	0.91	<0.005
(6) Brown trout	D	25.5	9	13	41.0 (39.0−43.0)	0.50 (0.37−0.63)	0.418 (0.0112)	$m=0.0154e^{-0.00100x}$	0.92	<0.005

[a] U, upstream section; D, downstream section.
[b] See Eq. 8 in text.
[c] Coefficient of determination for linear regression of $\log_e m$ vs. x (see Fig. 2B).
[d] Range of initial length and weight.
[e] Standard error of the mean.
[f] Fish acclimated 2 additional days to food (see text).
[g] Slope at 300 cm excluded as outlier.

using focal points near the substrate. The map provides conservative estimates for potential profit of the other 11 fish because most used small irregularities of the stream bed as refuges affording reduced swimming velocities, which would decrease swimming costs and increase potential profit.

Because fish were observed 6−10 h each day during the 9-day experiment the linear dominance hierarchy was known, and was nearly identical to the order when fish were ranked by their specific growth rates. The rank observed in the linear dominance hierarchy is indicated by the number circled at each fish position and preceding the fin-clip code (Fig. 7). Fish were similarly ranked according to predicted potential profit at their positions based on the map, the number shown after the fin-clip code. The two rankings are nearly identical and the correlation between them is highly significant ($r = 0.97$, $p << 0.001$) by Pearson's nonparametric test (Conover 1980), which indicates that the predicted position choice based on potential profit fits closely that observed. In turn, this suggests that these salmonids choose stream positions with respect to constraints of food supply, flow, and the dominance hierarchy.

The relationships between specific growth rate and net energy gain for stream salmonids may help validate the assumption stated above that maximizing net energy gain is equivalent to maximizing fitness. A problem in linking the two is that net energy gain is measured on the short term in calories per second or per hour, while fitness is a function of long-term reproductive success, requiring months or years to be expressed in most animals. Thus, most optimal foraging models fail to account for the additional factors involved in optimization on an evolutionary time scale, a problem described by Pyke et al. (1977).

Specific growth rate incorporates more of the factors that bear on fitness and is measured over a longer time scale than net energy gain usually is. Moreover, specific growth rate is expected to be closely correlated with fitness in fish, because fish that grow at the highest rates should have more energy to invest in reproduction and produce more offspring that survive. Therefore, positive relationships between specific growth rate and potential profit for salmonids lend power to the argument that dominant fish that maximize potential profit also maximize fitness.

Microhabitat selection by stream salmonids

The results of these experiments confirm ideas set forth by several investigators more than a decade ago about the mechanisms of microhabitat choice by stream salmonids. Everest and Chapman (1972) observed that juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*) consistently faced moderate current speeds yet were close to fast water, and proposed that such behavior should maximize the quantity of available drift while minimizing energy expenditure to remain at feeding stations. Everest and Chapman (1972) also showed that faster water delivered more drift per unit time in natural streams than slower water. Using these data (then unpublished) Chapman and Bjornn (1969) proposed that the main reason juvenile salmonids move into faster and deeper water as they grow is to exploit the greater rate of food supply there.

In a study of social behavior of adult brown trout and rainbow trout, Jenkins (1969) found that groups of fish set up linear dominance hierarchies and all fish preferred one most favorable position in each stream section. When the dominant fish was removed, the next fish in each hierarchy moved into the preferred position. Jenkins (1969) found that these preferred feeding positions were consistently located under principal surface drift patterns but were limited by subsurface velocities tolerable to the fish, which led him to propose that trout must be able to choose positions in the current which maximize food intake while minimizing energy expenditure.

Fausch and White (1981), using these ideas of favorable positions for stream salmonids and drawing from the methods of fish position measurement used by Griffith (1972), developed a simple measure of trout position quality called "water velocity difference" for use in a study of competition between adult brook trout and brown trout. Water velocity difference was defined as the difference between the maximum velocity within 60 cm of an adult trout and the focal point velocity, and thus incorporated the ideas of maximum net energy gain proposed by Jenkins (1969) and Everest and Chapman (1972).

The results of these experiments support the hypothesis that juvenile salmonids select focal points on the basis of water-velocity characteristics and food supply to maximize net energy gain. In specific stream sections, position choice is further constrained by formation of intraspecific hierarchies in which dominant fish hold optimal positions and, in turn, achieve the highest specific growth rates. Moreover, specific growth rates of all fish in the hierarchy are related to potential for net energy gain at their stream positions according to hyperbolic functions that can be described by the Michaelis–Menten model.

Acknowledgements

I am deeply grateful to Darrell King for introducing me to many of the ideas developed here and for frequent discussions on their merit. Ray White influenced my thinking about stream salmonid positions, and Earl Werner about foraging in fish. Financial support was provided by grant No. NA-80-AA-D-00072 (project No. R/GLF-6) from the Michigan Sea Grant Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and by the Michigan Agricultural Experiment Station. Phil Yant, Jim Karr, and Tom Schoener critically reviewed earlier drafts of the manuscript. I also thank Dr. T. G. Northcote and an anonymous reviewer for helpful comments.

Bliss, C. I., and A. T. James. 1966. Fitting the rectangular hyperbola. Biometrics, **22**: 573–602.

Brett, J. R. 1979. Environmental factors and growth. Fish Physiol. 1969, **8**: 599–675.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. **26**: 2363–2394.

Brocksen, R. W., G. E. Davis, and C. E. Warren. 1970. Analysis of trophic processes on the basis of density-dependent functions. *In* Marine food chains. *Edited by* J. H. Steele. University of California Press, Berkeley, CA. pp. 468–498.

Carline, R. F., and J. D. Hall. 1973. Evaluation of a method for estimating food consumption rates of fish. J. Fish. Res. Board Can. **30**: 623–629.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. *In* Symposium on Salmon and Trout in Streams. *Edited by* T. G. Northcote. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver. pp. 153–176.

Conover, W. J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley and Sons, New York.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. **18**: 1–158.

Dowd, J. E., and D. S. Riggs. 1965. A comparison of estimates of Michaelis–Menten kinetic constants from various linear transformations. J. Biol. Chem. **240**: 863–869.

Everest, F. H. 1967. Midget Bentzel current speed tube for ecological investigations. Limnol. Oceanogr. **12**: 179–180.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Boad Can. **29**: 91–100.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. **38**: 1220–1227.

——— 1983. Sinuous stream aquarium to simulate lotic fish habitat. Prog. Fish-Cult. **45**: 113–116.

Gibson, R. J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and steelhead trout (*Salmo gairdneri*), at the juvenile fluviatile stages. Can. Tech. Rep. Fish. Aquat. Sci. No. 1029.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. J. Fish. Res. Board Can. **29**: 265–273.

Grubbs, F. E., and G. Beck. 1972. Extension of sample sizes and percentage points for significance tests of outlying observations. Technometrics, **14**: 847–854.

Healey, F. P. 1980. Slope of the Monod equation as an indicator of advantage in nutrient competition. Microb. Ecol. **5**: 281–286.

Jenkins, T. M., Jr. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav. Monogr. **2**: 56–123.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Inst. Freshwater Res. Drottningholm, **39**: 55–98.

King, D. L. 1980. Some cautions in applying results from aquatic microcosms. *In* Microcosms in ecological research. DOE Symp. Ser. No. 52. pp. 164–191.

Kingsland, S. 1982. The refractory model: the logistic curve and the history of population ecology. Q. Rev. Biol. **57**: 29–52.

LaBarbera, M., and S. Vogel. 1976. An inexpensive thermistor flowmeter for aquatic biology. Limnol. Oceanogr. **21**: 750–756.

Lampert, W., and U. Schober. 1980. The importance of "threshold" food concentrations. *In* Evolution and ecology of zooplankton communities. Spec. Symp. Am. Soc. Limnol. Oceanogr. **3**: 264–267.

Leopold, L. B., and W. B. Langbein. 1966. River meanders. Sci. Am. **214**: 60–70.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology, **62**: 1370–1386.

Monod, J. 1949. The growth of bacterial cultures. Annu. Rev. Microbiol. **3**: 371–394.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. **52**: 137–154.

Ricker, W. E. 1979. Growth rates and models. Fish Physiol. 1969, **8**: 677–743.

Spotte, S. H. 1979. Fish and invertebrate culture: water management in closed systems. 2nd ed. John Wiley and Sons, New York.

Stauffer, G. D. 1973. A growth model for salmonids reared in hatchery environments. Ph.D. dissertation, University of Washington, Seattle, WA.

Stewart, D. J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modelling synthesis. Ph.D. dissertation, University of Wisconsin, Madison, WI.

Tilman, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology, **62**: 802–815.

Wankowski, J. W. J. 1981. Behavioural aspects of predation by juvenile Atlantic salmon (*Salmo salar* L.) on particulate, drifting prey. Anim. Behav. **29**: 557–571.

Ware, D. M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. **37**: 1012–1024.

Warren, C. E. 1971. Biology and water pollution control. W. B. Saunders Co., Philadelphia.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. **111**: 553–578.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology, **55**: 1042–1052.

——— 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology, **60**: 256–264.

WERNER, E. E., and G. G. MITTELBACH. 1981. Optimal foraging: field tests of diet choice and habitat switching. Am. Zool. **21**: 813–829.

YOUNG, T. C., and D. L. KING. 1980. Interacting limits to algal growth: light, phosphorus, and carbon dioxide availability. Water Res. **14**: 409–412.

[1985]

Environmental Biology of Fishes Vol. 14, No. 1, pp. 51–59, 1985
© Dr W. Junk Publishers, Dordrecht.

Distribution, biology and hybridization of *Scaphirhynchus albus* and *S. platorynchus* in the Missouri and Mississippi rivers

Douglas M. Carlson[1], William L. Pflieger, Linden Trial & Pamela S. Haverland
Missouri Department of Conservation, 1110 College Avenue, Columbia, MO 65201, U.S.A.
[1] *Present address: New York Department Environmental Conservation, Stamford, NY 12167, U.S.A.*

Keywords: Environmental effects, Food, Growth, Morphometric Comparisons, Status, Threats to survival

Synopsis

Scaphirhynchus albus and *S. platorynchus* were studied in Missouri during 1978–1979 to assess their distribution and abundance, to obtain information on their life histories, and to identify existing or potential threats to their survival. *S. platorynchus* was collected in substantial numbers (4355 specimens) at all 12 sampling stations in the Missouri and Mississippi rivers, while only 11 *S. albus* were captured from 6 stations. Twelve specimens identified in the field as hybrids between the two species were captured from 4 stations. Morphometric and meristic comparisons of presumed hybrids with the parent species, using cluster and principal components analyses, demonstrated intermediacy of most specimens identified in the field as hybrids. Aquatic insects comprised most of the diet of *S. platorynchus* and *S. albus*, but *S. albus* and the hybrids had consumed considerable quantities of fish. *S. albus* grew more rapidly than *S. platorynchus*, while the growth of hybrids was intermediate. Hybridization appears to be a recent phenomenon, resulting from man-caused changes in the big-river environment. Hybridization may be a threat to survival of *S. albus* in the study streams.

Introduction

The river sturgeons, *Scaphirhynchus albus* and *S. platorynchus*. are endemic to large rivers of the central United States, primarily in the Mississippi Basin (Bailey & Cross 1954). *S. platorynchus* occurs widely in the Mississippi River and its major tributaries, and is sympatric with *S. albus* in the middle and lower Mississippi, Missouri, and Yellowstone rivers.

S. platorynchus was abundant and supported a substantial commercial fishery in the early part of this century (Carlander 1954). Today, this fishery is reduced, but is still important locally (Helms 1974); *S. platorynchus* is still rather common over much of its range. *S. albus* was not recognized as a species until 1905 (Forbes & Richardson 1905), and has not been distinguished in commercial fishery reports. Perhaps it has never been especially abundant, and it is one of the lesser known freshwater fishes in North America (Kallemeyn 1983).

In Missouri, the most recent authenticated capture of *S. albus* prior to this investigation was in 1948 (Fisher 1962), and this species has been classified as endangered (Nordstrom et al. 1977). This study of *S. albus* was undertaken to better define its distribution and abundance within the state, to obtain information on its life history, and to identify existing or potential threats to its survival. Comparative information was obtained on *S. platorynchus* because of its close relationship to *S. albus*, and because of the opportunity for study afforded by the planned investigation of its more seriously threatened relative.

An unexpected result of this investigation was the capture of apparent hybrids between the two species. Although many hybrid combinations are known between species of sturgeons (Acipenseridae), none have been previously reported in the genus *Scaphirhynchus* (Schwartz 1972, 1981). In this report we document our findings concerning possible hybridization in this genus, and evaluate these findings with respect to the status and prospects for survival of *S. albus* in the lower Missouri and Mississippi rivers.

Materials and methods

Sturgeons were collected from 12 stations in the Missouri and Mississippi rivers, in and adjoining the state of Missouri (Table 1). Most sturgeons were obtained with trotlines, trammel nets, and dip nets. Trotlines were baited with worms and fished on the bottom over sandbars. Trammel nets were weighted and set to fish near the bottom behind wing dikes, or were drifted near the bottom in the main channel. At the Chain of Rocks station, sturgeons entrapped in the forebay of the St. Louis City water intake were collected by dip netting. These gear types were fished a total of 95 days during spring and fall of 1978 and 1979.

The fork length (FL) of all captured sturgeons were recorded, and most specimens were released. A representative series of 5-15 individuals from each station were retained for internal examination. From each of these fish, the gonads were examined to determine sex and reproductive condition, the stomach was preserved for food habit studies, and the first pectoral-fin ray was kept for aging. Some specimens were preserved whole for meristic and morphometric comparisons, and tissue samples from selected specimens were frozen for electrophoretic analysis.

In the laboratory, stomachs were transferred from the field preservative (10% formalin) to 70% ethanol. The volume of the stomach contents was determined, food items were sorted and identified to the lowest possible taxonomic level, and the percentage each comprised of the total volume was estimated visually. The quantities of material too far digested for identification, as well as earth-

Table 1. Numbers of *S. platorynchus*, *S. albus*, and presumed hybrids obtained at 12 stations on the Missouri and Mississippi rivers.

Station[1]	*S. platorynchus*	*S. albus*	Hybrids	Total
Missouri River				
Brownsville (RM 534)	481	2	0	483
St. Joseph (RM 461)	65	1	0	66
Kansas City (RM 360)	347	1	2	350
Brunswick (RM 258)	148	0	0	148
Easley (RM 172)	608	1	0	609
St. Louis (RM 16)	148	0	2	150
Mississippi River				
Canton (RM 341)	46	0	0	46
Saverton (RM 302)	331	0	0	331
Chain of Rocks (RM 188)	1800	0	7	1807
Ste. Genevieve (RM 118)	97	1	0	98
Cairo (RM 952)	196	5	1	202
Caruthersville (RM 852)	65	0	0	65
Totals	4332	11	12	4355

[1] Station location designated by nearest city and river mile (RM) of station midpoint, taken from U.S. Army Corps of Engineers navigation charts.

worms (from specimens caught on baited hooks) were excluded from food habit comparisons.

Pectoral-fin rays were sectioned, and the sections were cleared in xylene and emersed in glycerine for age determinations. Annuli were counted toward the anterior apex of the fin-ray section to minimize errors in counts (Sokolov & Akimova 1976), and ages were reported for fish size at time of capture.

To document possible hybridization and confirm field identifications, meristic and morphometric comparisons of preserved specimens were made, using techniques and characters proposed by Bailey & Cross (1954). Four fin-ray counts and 10 measurements were made on each specimen (see Table 2 for a list of characters). Measurements were converted to thousandths of standard length (SL). The development of scutes on the belly were quantified by establishing four character states and ranking them on a scale of 1–4. These character states were: (1) belly with a mosaic of well developed scutes; (2) belly as in (1), but with a naked strip anteriorly at the midline; (3) belly with a few widely scattered scutes; and (4) belly naked except for a few rudimentary scutes posteriorly.

Cluster analysis and principal components analysis were performed, using computer programs provided by SAS (Ray 1982). All characters (except standard length) listed in Table 2 were used as variables in each analysis unless otherwise noted. For all analyses, field identifications were used in designating specimens as *S. platorynchus, S. albus,* or hybrids.

Frozen tissue samples from 7 *S. platorynchus,* 10 *S. albus,* and 6 presumed hybrids were sent for electrophoretic analysis to the population genetics laboratory at the University of Montana. The findings of this analysis are reported in detail elsewhere (Phelps & Allendorf 1983).

Table 2. Univariate statistics and average coefficient of variation (C.V.) for two species of *Scaphirhynchus* and hybrids between them. Group assignments are based on field identifications. Morphometric characters are expressed as thousandths of standard length. $\bar{x}$ is mean, $s_{\bar{x}}$ standard error of the mean, and N is sample size.

Character	*S. platorynchus* N = 10		Hybrids N = 12		*S. albus* N = 8	
	$\bar{x} \pm 2s_{\bar{x}}$	C.V.	$\bar{x} \pm 2s_{\bar{x}}$	C.V.	$\bar{x} \pm 2s_{\bar{x}}$	C.V.
Meristic						
Dorsal-fin rays	32.4 ± 1.6	7.7	37.6 ± 1.5	6.8	38.4 ± 1.3	5.0
Anal-fin rays	20.3 ± 0.8	6.6	23.5 ± 0.7	5.3	24.5 ± 0.9	5.3
Pectoral-fin rays	40.9 ± 2.8	10.8	45.8 ± 2.1	8.1	46.0 ± 3.1	9.6
Pelvic-fin rays	26.8 ± 1.6	9.8	27.9 ± 1.1	6.6	30.5 ± 0.9	4.3
Belly scutellation	1.6 ± 0.6	60.4	3.0 ± 0.4	24.6	3.9 ± 0.2	9.1
Morphometric						
Head length	262.3 ± 6.9	4.1	281.1 ± 10.4	6.4	300.1 ± 8.8	4.1
Rostral length	179.0 ± 8.7	7.7	197.2 ± 6.2	5.5	205.4 ± 6.2	4.2
Orbital length	9.7 ± 2.2	35.4	11.6 ± 0.9	13.5	9.6 ± 1.9	28.8
Mouth width	75.0 ± 2.3	4.8	85.0 ± 3.4	6.9	93.1 ± 6.6	10.1
Snout to outer barbel	100.2 ± 3.4	5.3	119.0 ± 6.8	9.9	133.3 ± 5.1	5.4
Mouth to inner barbel	60.6 ± 3.3	8.5	59.2 ± 2.8	8.3	55.9 ± 2.5	6.4
Outer barbel length	84.6 ± 7.5	14.0	103.6 ± 7.7	12.9	114.6 ± 19.9	24.6
Inner barbel length	62.5 ± 3.9	10.0	65.1 ± 2.3	6.2	56.6 ± 7.7	19.2
Tenth lateral plate	46.7 ± 3.3	11.3	39.9 ± 1.1	4.7	34.9 ± 2.4	9.6
Average C.V.		14.0		9.0		10.4
Standard length (mm)	580.0		588.0		622.6	

Results

Identification and documentation of hybrids

We captured 4355 river sturgeons in this study. The field identifications of these specimens were: 4332 (99.5%) *S. platorynchus,* 11 (0.2%) *S. albus,* and 12 (0.3%) hybrids between the species (Table 1). Sturgeons were identified as hybrids because of intermediacy or inconsistency in the expression of certain characters (barbel placement and length, rostral shape and length, belly scutellation, and coloration) that are readily observed under field conditions. Specimens of the presumed hybrids and the parent species were subjected to morphometric, meristic, and biochemical comparisons to substantiate or refute the field identification.

Thirty river sturgeons ranging in standard length from 447 to 816 mm were used in comparisons. The presumptive identifications of these specimens were: 10 *S. platorynchus,* 8 *S. albus,* and 12 hybrids. In all characters except orbital length and inner barbel length, the mean for presumed hybrids was intermediate between the means for *S. platorynchus* and *S. albus* (Table 2). However, for most of these characters the hybrid mean was closer to that of *S. albus* than to that of *S. platorynchus.* The means for orbital length and inner barbel length were greater in the hybrids than in the two species. The presumed hybrids did not exhibit greater variability in most characters than did the species. In 9 of 14 characters and in the mean coefficient, *S. platorynchus* exhibited the highest coefficient of variation of the three sturgeon groups.

Cluster analysis, using all 14 characters listed in Table 2, produced a grouping of the specimens that is quite consistent with the field identifications (Fig. 1). When three clusters are assumed, 9 (90%) of 10 *S. platorynchus* were allocated to one cluster, 9 (75%) of 12 presumed hybrids were allocated to a second cluster, and 6 (75%) of 8 *S. albus* were allocated to a third cluster. Of the total sample of 30 specimens, 6 (20%) were allocated to a different group by cluster analysis than by the field identification.

Principal components were calculated for all characters, and the scores were plotted for the first two principal components (Fig. 2). This resulted in a complete separation of specimens identified as *S. platorynchus* from those identified as *S. albus,* with most of the presumed hybrids isolated between them. However, two specimens identified as hybrids are plotted within the *S. albus* group, while

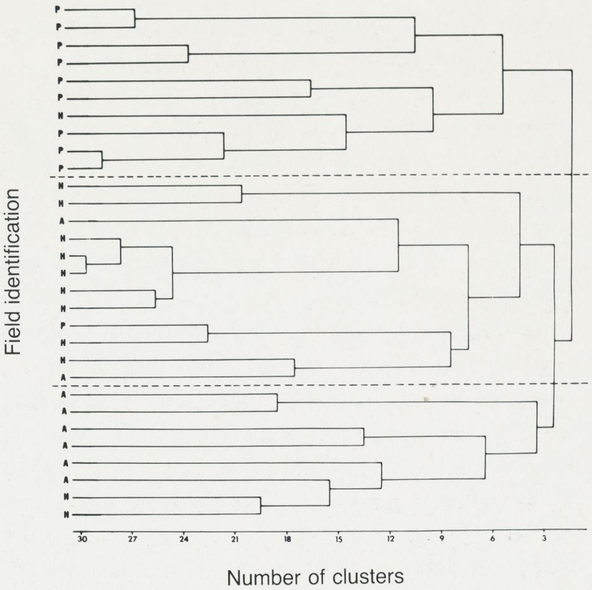


Fig. 1. Dendrogram for 30 *Scaphirhynchus,* produced by application of the SAS cluster procedure to 5 meristic and 9 morphometric characters. The field identifications of specimens were: P = *S. platorynchus,* A = *S. albus* and H = hybrid.

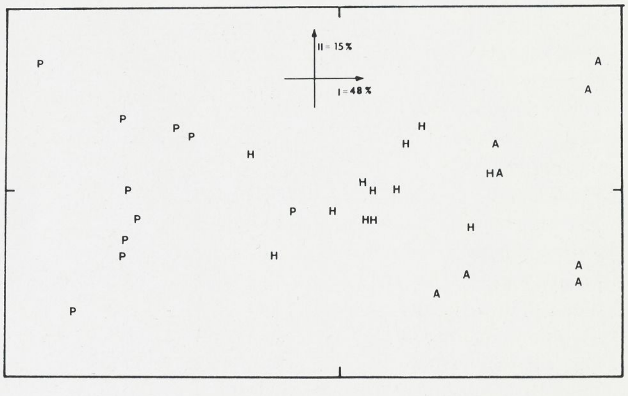


Fig. 2. Relative similarity of 30 *Scaphirhynchus,* as shown by projections on the first two principal components of the character correlation matrix for 5 meristic and 9 morphometric characters. The field identifications of specimens were: P = *S. platorynchus,* A = *S. albus,* and H = hybrid.

one *S. platorynchus* is within the hybrid group. One presumed hybrid was well separated from the hybrid group and near the *S. platorynchus* group.

The variation shown in Figure 2 accounts for $48 + 15 = 63\%$ of the total variance in the data matrix. All characters except orbital length and inner barbel length contributed significantly ($P<0.05$) to principal component 1 (Table 3). Five characters (pelvic-fin rays, orbital length, mouth to inner barbel, outer barbel length and inner barbel length) contributed significantly to principal component 2. Three of these characters contributed significantly to both components.

To provide some perspective for interpreting these results, we calculated principal components for 15 specimens longer than 250 mm SL listed by Bailey & Cross (1954). Since only morphometric characters were available for their fish, this required recomputing the principal components for our fish, using only morphometric characters.

When scores of the first two principal components are plotted as before, greater overlap is evident between the three sturgeon groups (Fig. 3) than was the case when all characters were used (Fig. 2). *S. platorynchus* and *S. albus* are still well separated, but the presumed hybrids more broadly overlap the plots for the two species.

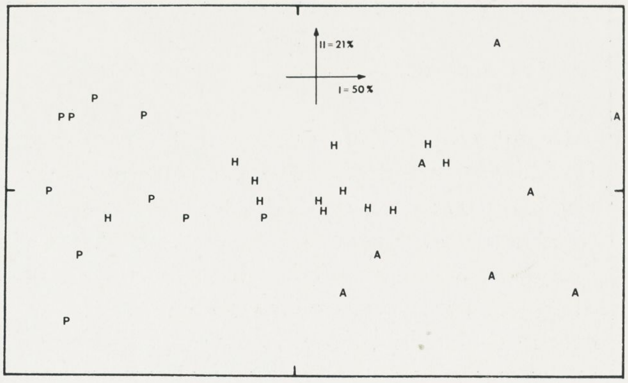


Fig. 3. Relative similarity of 30 *Scaphirhynchus,* as shown by projections on the first two principal components of the character correlation matrix for 9 morphometric characters. The field identifications of specimens were: P = *S. platorynchus,* A = *S. albus,* and H = hybrid.

When scores are plotted for the specimens of Bailey & Cross (1954), two widely separate groups, corresponding to *S. platorynchus* and *S. albus,* are evident (Fig. 4). The plot for the Bailey & Cross (1954) specimens appears comparable to the plot for specimens identified as *S. platorynchus* and *S albus* in our study. However, 9 of their 15 specimens were smaller than any used in our analysis,

Table 3. Correlation coefficients for the first two principal components of *Scaphirynchus* from the present study and from specimens examined by Bailey & Cross (1954). Significant correlations ($P<0.05$) are indicated by an asterisk.

Character	Present study				Bailey & Cross (1954)	
	All characters		Morphometric characters		Morphometric characters	
	Component 1	Component 2	Component 1	Component 2	Component 1	Component 2
Dorsal-fin rays	.79*	.18				
Anal-fin rays	.84*	−.03				
Pectoral-fin rays	.51*	−.03				
Pelvic-fin rays	.66*	−.42*				
Belly scutellation	.80*	−.16				
Head length	.82*	.02	.93*	−.05	.93*	−.04
Rostral length	.76*	−.25	.81*	−.27	.84*	−.40
Orbital length	−.06	−.68*	−.07	−.65*	−.48	−.73*
Mouth width	.85*	.31	.89*	.23	.85*	.18
Snout to outer barbel	.89*	−.06	.94*	−.15	.98*	−.06
Mouth to inner barbel	−.40*	.55*	−.30	.55*	−.84*	−.16
Outer barbel length	.68*	.64*	.70	.62	.41	.76*
Inner barbel length	−.13	.67*	−.18	.80*	−.89*	.26
Tenth lateral plate	−.78*	−.11	−.84*	−.04	−.87*	.33

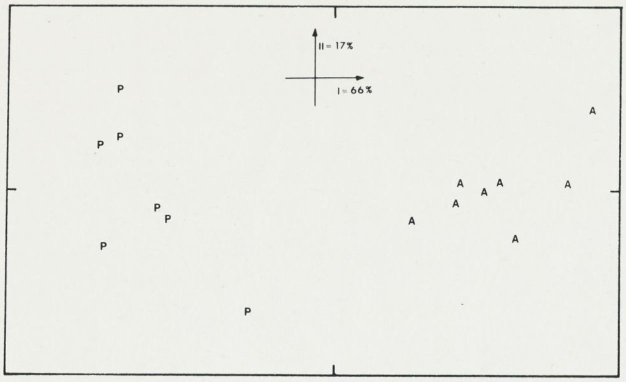


Fig. 4. Relative similarity of 15 *Scaphirhynchus*, as shown by projections on the first two principal components of the character correlation matrix for 9 morphometric characters. The identifications of specimens were: P = *S. platorynchus* and A = *S. albus*. The data for this analysis came from Bailey & Cross (1954).

and their smallest specimens exhibited the most intermediate principal component scores. Perhaps the separation between the species plots for their data would have been even greater if larger specimens had been available. There is general agreement between their data and our data in the contribution of various morphometric characters to component 1 and component 2 (Table 3). The major exceptions appear to involve characters relating to barbel position and length.

Electrophoretic analysis revealed that *S. platorynchus* and *S. albus* were indistinguishable at all 37 loci examined (Phelps & Allendorf 1983). Also, at three polymorphic loci, *S. albus* and *S. platorynchus,* and geographically distant populations of the latter species, exhibited no statistically significant differences in morph frequency. Therefore, electrophoresis provided no supportive evidence for or against the identification of some specimens as hybrids. The similarity at such a large number of loci suggests a close genetic relationship between these two species. This result is surprising, considering the many phenotypic differences between them.

Distribution, relative abundance, and habitat

S. platorynchus occurs throughout the Missouri and Mississippi rivers in Missouri, and was captured in substantial numbers at all 12 stations (Table 1). This species comprised 73% of all fishes in our collections. However, our sampling techniques and gear were intentionally selective for sturgeons.

S. albus was recorded at 6 of 12 stations, and 11 specimens were captured. The largest number of specimens (5) were from the Mississippi River at Cairo, where this species comprised 2.5% of the river sturgeons in our collections. The proportions of *S. albus* in collections from other stations were: Brownsville – 0.4%, St. Joseph – 1.5%, Kansas City – 0.3%, Easley – 0.2%, and Ste. Genevieve – 1.0%. No *S. albus* were captured from the Mississippi River upstream from the mouth of the Missouri River.

Twelve sturgeons identified as hybrids were collected from four stations. The most specimens (7) came from Chain of Rocks on the Mississippi River. At that station they comprised 0.4% of the river sturgeons captured. The proportions of hybrids at other stations were: Kansas City – 0.6%, St. Louis – 1.3%, and Cairo – 0.5%.

Both *S. platorynchus* and *S. albus* were found in the main channels of the river, along sandbars at the inside of river bends and behind wing dikes with deeply scoured trenches. *S. albus* was generally taken in gear-sets (usually trotlines) that contained *S. platorynchus,* but four of eleven specimens were caught in areas with swift current where *S. platorynchus* was less numerous. Sturgeons identified as hybrids appeared to be more closely associated with *S. platorynchus* than with *S. albus*. On the average, each gear-set that caught a hybrid contained 14 *S. platorynchus,* compared with an average of two *S. platorynchus* for gear-sets that caught *S. albus*.

Food, growth, and sex ratio

Aquatic invertebrates (principally the immature stages of insects) comprised most of the diet of river sturgeons captured in this study, but with a greater proportion of fish (mostly cyprinids) in the diet of *S. albus* and presumed hybrids than in *S. platorynchus* (Table 4). These differences in the consumption of fish were evident in both volume ($T_{P\text{-}A}$

-2.5, df = 8) and frequency of occurrence ($X^2_{P\text{-}A} = 36.4$, df = 1; $X^2_{P\text{-}H} = 5.7$, df = 1). Coker (1930) and Cross (1967) also reported a high incidence of fish in the diet of *S. albus,* while other investigators (Held 1969, Walberg et al. 1971, Helms 1974, Modde & Schmulbach 1977, Durkee et al. 1979) reported a low incidence of fish (less than 2% by volume) in the diet of the *S. platorynchus.* Sand occurred frequently in the stomachs examined (frequency of occurrence 24.6% for all specimens combined) and was probably consumed incidentally along with food items. The occurrence of plant material in the stomachs may also have been incidental.

The length of *S. albus* was significantly greater than that of *S. platorynchus* (T = 4.77, df = 6) for each age group in which comparable data was available, while the hybrids were generally intermediate in length (Fig. 5). Fogle (1963) also reported more rapid growth in *S. albus* than in *S. platorynchus.*

Females predominated over males in our samples of *S. platorynchus* and *S. albus,* with males comprising 27% and 33%, respectively of all the specimens examined. Three percent of the *S. platorynchus* were hermaphrodites. All 12 of the presumed hybrids were females.

Discussion

These analyses show that *S. albus* and *S. platorynchus* hybridize. Specimens tentatively identified as hybrids in the field were intermediate in several meristic and morphometric characters. The hybrids appeared to be more like *S. platorynchus* in habitat selection, but their diet resembled that of *S. albus* in containing a substantial quantity of fish. The growth rate of hybrids was intermediate between that of the parent species. All of the hybrids were females, possibly indicating an unbalanced sex ratio, as has been reported in some other fish hybrids (Hubbs 1955).

A principal components analysis of morphometric data presented by Bailey & Cross (1954) demonstrated that their sample included two mor-

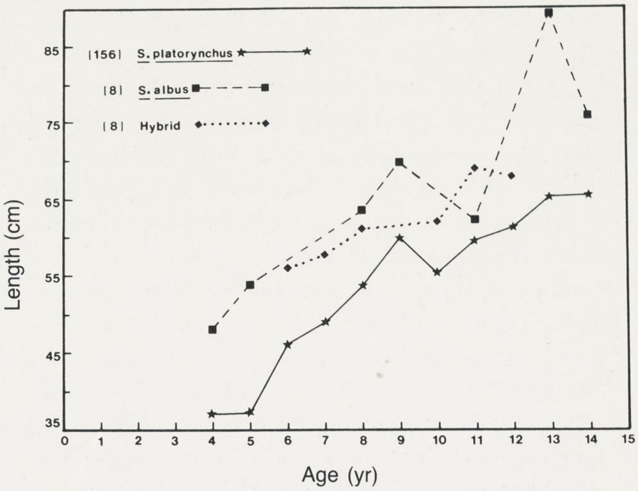


Fig. 5. Average length (FL) at each age for 172 *Scaphirhynchus* from the Missouri and Mississippi rivers.

Table 4. Composition by volume and frequency of occurrence of food categories in the diet of *S. platorynchus* (N = 234), *S. albus* (N = 9) and presumed hybrids (N = 9).

Food category	Composition by volume (%)			Frequency of occurrence (%)		
	S. platorynchus	Hybrids	*S. albus*	*S. platorynchus*	Hybrids	*S. albus*
Ephemeroptera	17.3	16.5	6.0	55.1	88.9	44.4
Odonata	7.3	5.3	8.6	18.4	11.1	33.3
Plecoptera	3.4	2.2	0.0	16.7	22.2	0.0
Trichoptera	34.0	4.8	37.8	74.8	44.4	55.6
Diptera	19.1	4.9	3.0	81.2	77.8	44.4
Other insects	11.8	2.8	2.9	44.9	22.2	33.3
Other invertebrates	2.0	4.6	1.3	15.8	66.7	33.3
Fish	1.6	31.3	37.7	4.3	22.2	55.6
Plant material	3.4	27.6	2.6	39.7	22.2	55.6

phologically distinct types of *Scaphirhynchus,* while a comparable analysis of our specimens demonstrated that they were not similarly separable into two types. The failure of Bailey & Cross (1954) and other workers to report hybrids between the species of *Scaphirhynchus* may indicate that hybridization is a recent phenomenon, resulting from a fundamental change in the behavioral and ecological relationships between these species. These changes may be related to man-induced reductions in habitat diversity and measureable changes in environmental parameters such as turbidity, flow regimens and substrate types. Projects by the U.S. Army Corps of Engineers designed to deepen and stabilize the lower Missouri River have reduced the water surface area by 50% and largely eliminated the numerous islands and side channels that were formerly present (Funk & Robinson 1974). Six large mainstem reservoirs constructed on the upper river have modified the natural seasonal flood patterns and resulted in measurable reductions in turbidity all the way to the river mouth (Neel et al. 1963, Whitley & Campbell 1973). Similar changes are evident in the Mississippi River downstream from the mouth of the Missouri. Schmulbach (1974) in discussing suspected hybridization between *Stizostedion canadense* and *S. vitreum* in the Missouri River, South Dakota stated that hybridization between species seems to be limited to places where man or nature has 'hybridized the habitat'. He concluded that the Missouri River is such a hybridized habitat.

Presumed hybrids were as prevalent in our samples as *S. albus,* suggesting that hybridization between the species of *Scaphirphynchus* may occur frequently. This hybridization could present a threat to survival of *S. albus,* through genetic swamping if the hybrids are fertile, and through competition for a limited habitat. Studies are needed to determine fertility of the hybrids and the extent and consequences of backcrossing.

Acknowledgements

Funds for this study were provided by the Office of Endangered Species, U.S. Fish and Wildlife Service (Endangered Species Project SE-1-6) and the Missouri Department of Conservation. We thank Mike Petersen for assistance in the field and laboratory, Stevan R. Phelps for doing the electrophoretic analysis, Frank B. Cross for loaning specimens, and Reeve M. Bailey for providing unpublished data. Joe G. Dillard, Thomas R. Russell, and Walter T. Keller reviewed early drafts of the manuscript.

References cited

Bailey, R.M. & F.B. Cross. 1954. River sturgeons of the American genus *Schaphirhynchus:* characters, distribution, and synonomy. Pap. Mich. Acad. Sci., Arts, Let. 39: 169–208.

Carlander, H.B. 1954. A history of fish and fishing in the Upper Mississippi River. Spec. Publ., Upper Miss. R. Cons. Comm. 96 pp.

Coker, R.E. 1930. Studies of common fishes of the Mississippi River at Keokuk. U.S. Bur. Fish. Bull. 45: 141–225.

Cross, F.B. 1967. Handbook of fishes of Kansas. Mus. Nat. Hist. Univ. Kans., Misc. Publ. 45: 1–357.

Durkee, P., B. Paulson & R. Bellig. 1979. Shovelnose sturgeon (*Scaphirhynchus platorynchus*) in the Minnesota River. Minn. Acad. Sci. 45(2): 18–20.

Fisher, H.J. 1962. Some fishes of the lower Missouri River. Amer. Midl. Nat. 68: 424–429.

Fogle, N.E. 1963. Report of fisheries investigations during the fifth year of impoundment of Oahe Reservoir, South Dakota 1962. South Dakota Dept. Game Fish and Parks. D-J Proj. F-1-R-12, Job 10-12. 35 pp.

Forbes, S.A. & R.E. Richardson. 1905. On a new shovelnose sturgeon from the Mississippi River. Bull. Ill. State Lab. Nat. Hist. 7: 37–44.

Funk, J.L. & J.W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Mo. Dept. Cons. Aquatic Ser. 11. 52 pp.

Held, J.W. 1969. Some early summer foods of the shovelnose sturgeon in the Missouri River. Trans. Amer. Fish. Soc. 98: 514–517.

Helms, D.R. 1974. Shovelnose sturgeon, *Scaphirhynchus platorynchus* (Rafinesque) in the navigational impoundments of the Upper Mississippi River. Iowa Cons. Comm. Tech. Ser. 74–3. 68 pp.

Hubbs, C.L. 1955. Hybridization between fish species in nature. Syst. Zool. 4: 1–20.

Kallemeyn, L. 1983. Status of the pallid sturgeon. Fisheries 8: 3–9.

Modde, T. & J.C. Schmulbach. 1977. Food and feeding behavior of the shovelnose, sturgeon, *Scaphirhynchus platorynchus,* in the unchannelized Missouri River, South Dakota. Trans. Amer. Fish. Soc. 106: 602–608.

Neel, J.K., H.P. Nicholson & A. Hirsch. 1963. Main stem reservoir effects on water quality in the central Missouri

River. U.S. Dept. Health, Education, and Welfare Publ., Kansas City. 112 pp.

Nordstrom, G.R., W.L. Pflieger, K.C. Sadler & W.H. Lewis. 1977. Rare and endangered species of Missouri. Mo. Dept. Cons., Jefferson City. 129 pp.

Phelps, S.R. & F. Allendorf. 1983. Genetic identity of pallid and shovelnose sturgeon (*Scaphirhynchus albus* and *S. platorynchus*). Copeia 1983: 696–700.

Ray, A.R. 1982. SAS user's guide: statistics, 1982 edition. SAS Institute, Cary. 584 pp.

Schmulbach, J.C. 1974. An ecological study of the Missouri River prior to channelization. S. Dak. Water Resources Proj. P-024, Univ. S. Dak. Completion Rep. 34 pp.

Schwartz, F.J. 1972. World literature to fish hybrids with an analysis by family, species, and hybrid. Publ. Gulf Coast Res. Lab. Mus. 3: 1–328.

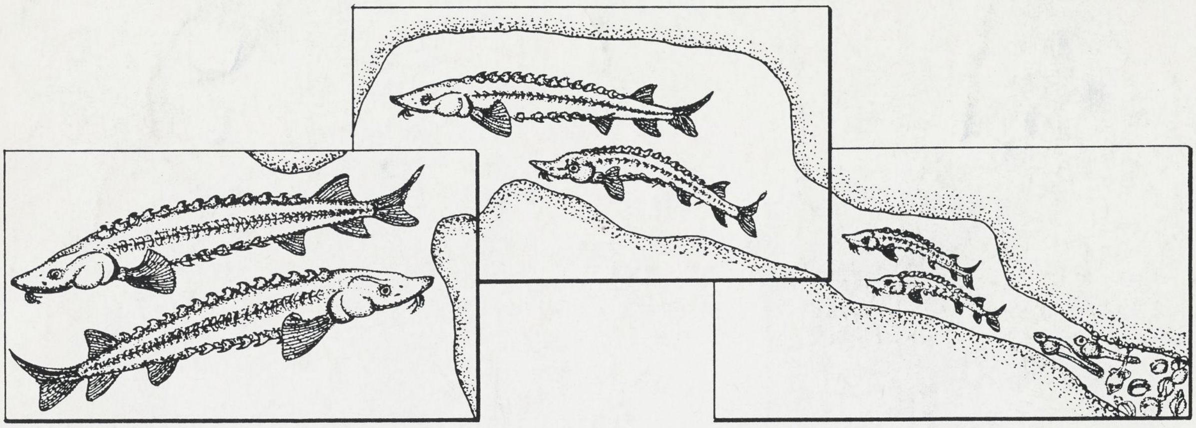
Schwartz, F.J. 1981. World literature to fish hybrids with an analysis by family, species, and hybrid: Supplement 1. NOAA Tech. Rep. NMFS SSF 750: 1–507.

Sokolov, L.I. & N.V. Akimova. 1976. Age determination of the Lena River sturgeon *Acipenser baeri.* J. Ichthyol. 16: 773–778.

Walburg, C.H., G.L. Kaiser & P.L. Hudson. 1971. Lewis and Clark Lake tailwater biota and some relations of the tailwater and reservoir fish population. pp. 449–467. *In:* G.E. Hall (ed.) Reservoir Fisheries and Limnology, Amer. Fish. Soc. Spec. Publ. 8, Bethesda.

Whitley, J.R. & R.S. Campbell. 1973. Some aspects of water quality and biology of the Missouri River. Trans. Mo. Acad. Sci. 7–8: 60–72.

Received 15.5.1984 *Accepted 15.1.1985*



Sturgeon spawning occurs primarily in large rivers. The embryos hatch in 7 to 15 days depending on temperature. The young fish are found in the river and estuary until late fall at which time they migrate to deeper waters.

Schelnas

QH
75
A1
N32
1986

chapter 1

BIODIVERSITY

E. O. Wilson, *Editor*
Frances M. Peter, *Associate Editor*

NATIONAL ACADEMY PRESS
Washington, D.C. 1988

CHAPTER

1

THE CURRENT STATE OF BIOLOGICAL DIVERSITY

E. O. WILSON
Frank B. Baird, Jr. Professor of Science, Harvard University,
Museum of Comparative Zoology, Cambridge, Massachusetts

Biological diversity must be treated more seriously as a global resource, to be indexed, used, and above all, preserved. Three circumstances conspire to give this matter an unprecedented urgency. First, exploding human populations are degrading the environment at an accelerating rate, especially in tropical countries. Second, science is discovering new uses for biological diversity in ways that can relieve both human suffering and environmental destruction. Third, much of the diversity is being irreversibly lost through extinction caused by the destruction of natural habitats, again especially in the tropics. Overall, we are locked into a race. We must hurry to acquire the knowledge on which a wise policy of conservation and development can be based for centuries to come.

To summarize the problem in this chapter, I review some current information on the magnitude of global diversity and the rate at which we are losing it. I concentrate on the tropical moist forests, because of all the major habitats, they are richest in species and because they are in greatest danger.

THE AMOUNT OF BIOLOGICAL DIVERSITY

Many recently published sources, especially the multiauthor volume *Synopsis and Classification of Living Organisms*, indicate that about 1.4 million living species of all kinds of organisms have been described (Parker, 1982; see also the numerical breakdown according to major taxonomic category of the world insect fauna prepared by Arnett, 1985). Approximately 750,000 are insects, 41,000 are vertebrates, and 250,000 are plants (that is, vascular plants and bryophytes). The remainder consists of a complex array of invertebrates, fungi, algae, and microorganisms (see Table 1-1). Most systematists agree that this picture is still very incomplete except

QH
540
P7
19:3

Prairie Nat. 19(3):173-176. 1987.

Faunal Exchange Between the Niobrara and White River Systems Of the North American Great Plains

RICHARD L. MAYDEN
Department of Biology, P.O. Box 1927, The University of Alabama
Tuscaloosa, AL 35487-1927

ABSTRACT — New records of the plains topminnow, *Fundulus sciadicus*, and the bigmouth shiner, *Notropis dorsalis*, are reported from LaCreek area in southern Bennett County, South Dakota. LaCreek stream is a tributary of the Little White River which drains directly into the Missouri River. The nearest populations of both of these species are in the nearby but separate drainage, Niobrara River and tributaries. A stream capture between Spring Creek of the White River and Minnechaduza Creek of the Niobrara River is hypothesized to explain the existing distributions of these fishes. Presumably, portions of the headwaters of Little White River formally flowed southward into the Niobrara River.

The natural process of stream capture is frequently considered by aquatic biologists interested in distributional patterns, biogeography, and community ecology. This phenomenon is a means of exchanging faunas and floras between river systems and is frequently employed as an explanation for the occurrence of an aquatic or semi-aquatic organism in a drainage atypical for the species. Drainage connections via stream capture have been commonly used in the ichthyological literature (see Hocutt and Wiley 1986 for review) as a means to explain some distributional patterns of fishes. Inter-drainage exchange of fishes has also been considered a means of producing disjunct populations of species which could then diverge from an ancestral condition. For the biogeographer, because we lack precise geological information on previous landscapes, specific faunal data represent some of the most important evidence of previous drainage connection. This is especially true for North American river drainages existing prior to the Pleistocene. Most information relates to major riverways, and even here flow patterns and connections are sometimes equivocal. Occasionally, stream captures are identified from existing stream channel topology and water flow patterns, such as one suggested by Bailey and Allum (1962), between the Little Missouri and the Belle Fourche rivers. This capture is a classic example, identified by the abrupt southwest bend of the Belle Fourche River, an ancestral section of the Little Missouri River. Biogeographically, this proposed capture is also supported by distributions of some fishes (Bailey and Allum 1962).

Below, I hypothesize a stream capture event between the Niobrara River system in Nebraska and South Dakota and the White River system in South Dakota. Both rivers form major western tributaries of the Missouri River in the Great Plains and have their headwaters in close proximity, while their mouths are widely disjunct. The age of this river connection is unknown, but it is supported by data from stream topology, regional topography, and faunal data.

Topographic Evidence

The area in which the hypothesized stream capture occurred is illustrated in Fig. 1. Involved are Minnechaduza Creek, a southeast-flowing tributary of the Niobrara River, and Spring Creek of the Little White River, a northward-flowing tributary of the Little White River in southern South Dakota. Minnechaduza Creek begins in Todd County, SD, less than 1 km from the headwaters of Spring Creek and less than 6 km southeast of a sharp bend in the Little White River (1:24,000 USGS Topographic sheet; Spring Creek sheet, 1969). This sharp bend in the Little White River represents the area of capture. The sharp change in direction of the Little White river is apparently not structurally controlled. This region is relatively flat with very little relief, except for occasional dunes and a relatively broad channel extending from the southeastern bend of the Little White River to the headwaters of Minnechaduza Creek (Fig. 1). Further, indicative of a previous continuous flow between these two drainages is the presence of isolated bodies of water in this broad channel, representing remnants of previous continuous waterway.

Northwest of the above mentioned river connection exists a similar condition between a portion of the Little White River and Bear-in-the-Lodge Creek (Fig. 1). Based on topographic maps (1:250,000 USGS Topographic sheets: Martin, 1967; Hot Springs, 1964. 1:100,000 Topographic sheets: Martin, 1983; Hot Springs, 1985; Pine Ridge, 1985) a relatively broad river channel can be traced extending from the headwaters of Minnechaduza Creek of the Niobrara River to Bear-in-the-Lodge Creek of the White River. In addition, between these two creeks several unnamed creeks also have their origins in this channel, and numerous endorheic lakes and ponds exist.

Thus, these data suggest that the Niobrara River system may have previously extended farther to the north and west than evidenced today. Included in the northwestern Niobrara is the present Minnechaduza Creek, upper White River, and perhaps Bear-in-the-Lodge Creek. With these limited data the determination of the exact date of the fracturing of the drainage is impossible.

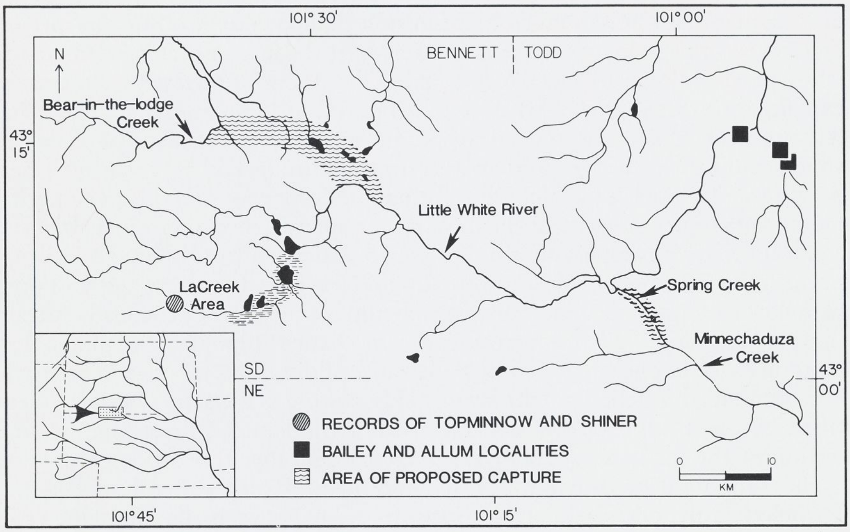


Figure 1. Map of region where hypothesized stream capture occurred between the Little White River and Minnechaduza Creek. Waved pattern represents area of proposed capture and presumed previous stream channels. Solid squares nearest localities where Bailey and Allum (1962) sampled but did not find *Fundulus sciadicus* or *Notropis dorsalis*. Circle represents new locality for *F. sciadicus* and *N. dorsalis* in LaCreek system. Inset map identifies location of map and drainage systems involved in proposed capture.

[1987]
E Science Serv

(O[illegible] to [illegible])

Biological Conservation 39 (1987) 269–289

Biology of The Nile Perch *Lates niloticus* (Pisces: Centropomidae) with Reference to its Proposed Role as a Sport Fish in Australia

Christopher G. Barlow

Fisheries Research Branch, Department of Primary Industries (Queensland),
Walkamin Research Station, Walkamin, Qld, 4872, Australia

&

Allan Lisle

Biometry Branch, Department of Primary Industries (Queensland),
Oonoonba Veterinary Laboratory, PO Box 1085, Townsville, Qld, 4810, Australia

(Received 4 June 1986; accepted 8 August 1986)

ABSTRACT

The Nile perch Lates niloticus *has been proposed for introduction to Australia to establish sport fisheries in tropical impoundments. Three lines of evidence suggest that the introduction would be potentially disastrous for Australian aquatic fauna. The lower temperature tolerance of the species and analysis of water temperatures in rivers of eastern Australia indicate that its range would extend to temperate regions in the country, thus endangering established fisheries for native species. The introduction of the Nile perch, an opportunistic predator, to Lake Victoria and Lake Kyoga in eastern Africa has caused a drastic decrease in species diversity and fish biomass.* L. niloticus *is not restricted to lacustrine habitats, and its biology indicates that it could colonise and adversely affect the fauna in a broad range of freshwater habitats in Australia. The risks associated with the proposed introduction are considered to outweigh the potential benefits. Consequently, the agency responsible for the evaluation programme has abandoned the concept of introducing the Nile perch to Australia.*

Biol. Conserv. 0006-3207/87/$03·50 © Elsevier Applied Science Publishers Ltd, England, 1987. Printed in Great Britain

1988
JSTOR

Copeia, 1988(1), pp. 153–173

Systematics of the *Notropis zonatus* Species Group, with Description of a New Species from the Interior Highlands of North America

RICHARD L. MAYDEN

The cardinal shiner, *Notropis cardinalis*, is described as a new member of the subgenus *Luxilus* in the *zonatus* species group. It is restricted to the Arkansas and Red river drainages in the Interior Highlands of North America. The new species differs from its close relatives *N. pilsbryi* and *N. zonatus* primarily in breeding color patterns, but it is also distinguished by meristic and morphometric features. Distributions of morphological characters of members of the *zonatus* group are congruent with previously described patterns of genic variation and support the recognition of three species in the Interior Highlands. Phylogenetic analysis of morphological and allozyme characters suggest that *N. cardinalis* and *N. pilsbryi* are sister species, and both are in turn sister to *N. zonatus.*

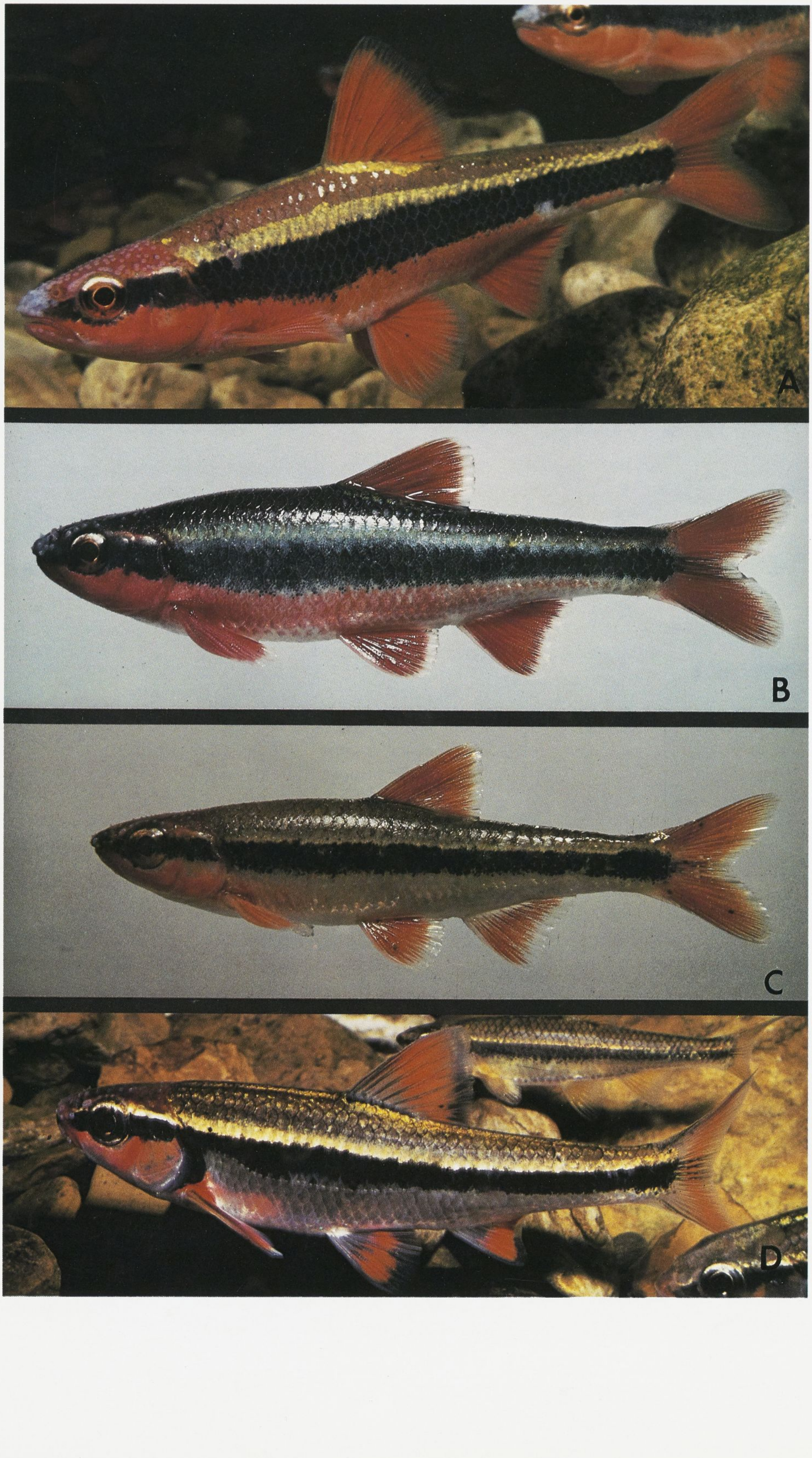
THE cyprinid subgenus *Luxilus* of *Notropis* has received considerable taxonomic and systematic attention, probably more than any other species group within the genus. Most of these research efforts have focused on the *zonatus* species group of the highland streams west of the Mississippi River and east of the Great Plains, most commonly referred to as the Interior Highlands. Since the descriptions of *Notropis zonatus* and *N. pilsbryi,* researchers have disagreed as to the number of species involved. Hubbs and Ortenburger (1929) and Hubbs and Brown (1929) placed the two species in synonymy and Hubbs and Moore (1940) considered the two to represent a single, polytypic species. Menzel and Cross (1977, systematics of the bleeding shiner species group [Cyprinidae: genus *Notropis,* subgenus *Luxilus.* Abstract given at the American Society of Ichthyologists and Herpetologists meeting in Gainesville, Florida in 1977.]) examined variation of secondary sexual characteristics and allozymes and concluded that a two species concept for the *zonatus* species group was untenable and that either a single, polytypic species should be recognized or three species (F. B. Cross, pers. comm.). Gilbert (1964), Pflieger (1971, 1975), and Buth (1979), however, considered the morphological and biochemical patterns of variation between *N. zonatus* and *N. pilsbryi* and other members of the subgenus to support the recognition of two distinct and evolutionarily independent species. More recently, Buth and Mayden (1981) examined allozyme variation among populations throughout the ranges of the two forms in order to determine if evidence of intergradation exists, which in turn would support the concept of a single species. Their study supported the validity of *N. zonatus* and *N. pilsbryi.* Buth and Mayden (1981) further concluded that previous studies supporting the single species hypothesis were either completely compatible with the two species hypothesis or conclusions of integradation were based on primitive characters for the subgenus *Luxilus* (characters inherited from ancestors) and were not reliable as indicators of gene flow.

Data employed in the above mentioned studies mainly included morphological characters from preserved museum specimens and allozyme data. Little information has been accumulated in terms of populational variation of breeding coloration and multivariate analyses of morphometric data. These data and analyses are presented herein. Detailed examination of breeding characteristics and morphometric variation among populations of the *zonatus* species group do not support a single species hypothesis and are in agreement with the recognition of *N. zonatus* and *N. pilsbryi.* Further, these data support the recognition of a new species from the Arkansas and Red river drainages, which is here described and distinguished from its closest relative, *N. pilsbryi.* Species accounts for *N. pilsbryi* and *N. zonatus* are presented, as well as discussions of species relationships and biogeography of the three species.

METHODS

Institutional abbreviations are as listed in Leviton et al. (1985), except for The University

© 1988 by the American Society of Ichthyologists and Herpetologists


A
B
C
D

Wildl. Soc. Bull. 21:509–514, 1993

[1993]
Jstor

"IN MY OPINION . . ."

MANAGING BIOLOGICAL DIVERSITY

FRED B. SAMSON, *U.S. Forest Service, Northern Region, Missoula, MT 59807*

FRITZ L. KNOPF, *National Biological Survey, National Ecology Research Center, Fort Collins, CO 80525-3400*

Biological diversity is the variety of life and accompanying ecological processes (Off. Technol. Assess. 1987, Wilcove and Samson 1987, Keystone 1991). Conservation of biological diversity is a major environmental issue (Wilson 1988, Counc. Environ. Quality 1991). The health and future of the earth's ecological systems (Lubchenco et al. 1991), global climate change (Botkin 1990), and an ever-increasing rate in loss of species, communities, and ecological systems (Myers 1990) are among issues drawing biological diversity to the mainstream of conservation worldwide (Int. Union Conserv. Nat. and Nat. Resour. [IUCN] et al. 1991).

The legal mandate for conserving biological diversity is now in place (Carlson 1988, Doremus 1991). More than 29 federal laws govern the use of biological resources in the United States (Rein 1991). The proposed National Biological Diversity Conservation and Environmental Research Act (H.R. 585 and S. 58) notes the need for a national biological diversity policy, would create a national center for biological diversity research, and recommends a federal interagency strategy for ecosystem conservation.

There are, however, hard choices ahead for the conservation of biological diversity, and biologists are grappling with how to set priorities in research and management (Roberts 1988). We sense disillusion among field biologists and managers relative to how to operationally approach the seemingly overwhelming charge of conserving biological diversity. Biologists also need to respond to critics like Hunt (1991) who suggest a tree farm has more biological diversity than an equal area of old-growth forest.

At present, science has played only a minor role in the conservation of biological diversity (Weston 1992) with no unified approach available to evaluate strategies and programs that address the quality and quantity of biological diversity (Murphy 1990, Erwin 1992). Although actions to conserve biological diversity need to be clearly defined by viewing issues across biological, spatial, and temporal scales (Knopf and Smith 1992), natural resource managers find much conflicting information in the literature on strategies and programs for the conservation of biological diversity (Ehrlich 1992). Moreover, recommendations provided in much of the published information available for planning or decisions not only can be debated but may prove counterproductive if implemented (Murphy 1989).

Current operational efforts beg for clearer focus on fundamental concepts central to daily decisions that impact native biological diversity. Recognizing that many biologists would provide different council and at the risk of oversimplification, we offer the following 4 topical issues as fundamental guidance to wise conservation action. These recommendations are based on our collective experiences working within conservation agencies since our original, collaborative essay (Samson and Knopf 1982). They are offered as initial, rather than authoritative, steps to better align research and management decisions with what we perceive as the critical issues in conserving biological diversity at the landscape and ecosystem levels of resolution.

UNDERSTAND ALPHA AND BETA DIVERSITY

Alpha diversity is the number of species within a habitat. Beta diversity is change or turnover in species across space. Biologists easily can manage a site for the maximum benefit to wildlife as indexed by the number of species present. This alpha diversity approach uses the index of species richness and is akin to traditional wildlife "enhancement" activities. Less attended to and understood is that a greater number of species can be actually "conserved" by incorporating beta diversity (Pimm and Gittleman 1992). Conserving areas with high species richness is of little value if they share the same set of species (Magurran 1988). Managing for remnants of natural ecosystems that share few species, i.e., that have a high beta diversity, will conserve more species (Harrison et al. 1992).

Incorporating beta diversity measurements into management decisions is illustrated in our original 2 case studies (Samson and Knopf 1982). An alpha diversity approach to management of tallgrass prairie relicts in central and southwestern Missouri leads to increases in habitat diversity and avian species richness, particularly in use by the brown-headed cowbird (*Molothrus ater*), field sparrow (*Spizella pusilla*), northern bobwhite (*Colinus virginianus*), red-winged blackbird (*Agelaius phoeniceus*), common grackle (*Quiscalus quiscula*), brown thrasher (*Toxostoma rufum*), and blue jay (*Cyanocitta cristata*).

Understanding how species are distributed among vegetation communities through beta diversity leads to an alternate approach to managing tallgrass prairie relicts. Certain species—for example, the greater prairie chicken (*Tympanuchus cupido*)—are closely associated with large, less habitat diverse, tallgrass prairie relicts. Management for both—the large, less habitat diverse and the small, more habitat diverse relicts—favors the greatest regional diversity.

The avifauna associated with 6 forest communities of Jackson Hole, Wyoming (Salt 1957), provided a second case study (Samson and Knopf 1982). As a first step, we calculated an index to alpha diversity for each plant community. With alpha diversity, the conclusion is that flatland-aspen (*Populus tremuloides*) and spruce-fir (*Picea-Abies*) forests should receive management priority because they had high species richness.

In contrast, beta diversity analysis showed remarkable similarity in species composition between willow-sedge (*Salix-Carex*) riparian, shrub-meadow, and flatland-aspen sites, with little need for narrow management of the deciduous communities to a single vegetation type. Further beta diversity analysis of lodgepole pine (*Pinus contorta*) forest, spruce-fir forest, and the lodgepole-spruce-fir ecotone showed a small but distinctive set of species associated with the lodgepole forest. Five of 8 species found in the lodgepole forest are restricted to western North America versus 6 of 19 species in the spruce-fir forest, and 8 of 25 species recorded in the deciduous forests. We conclude that forest management in the Jackson Hole area for lodgepole pine, spruce-fir, and deciduous areas will favor a diverse avifauna, particularly for those species unique to the West.

EMPHASIZE BIOTIC INTEGRITY

A growing number of ecologists suggest that biological immigrants—exotics and those species beyond their historical range—pose what may be the most significant threat to the continuing loss of biological diversity (Knopf 1986,