INFORMATION

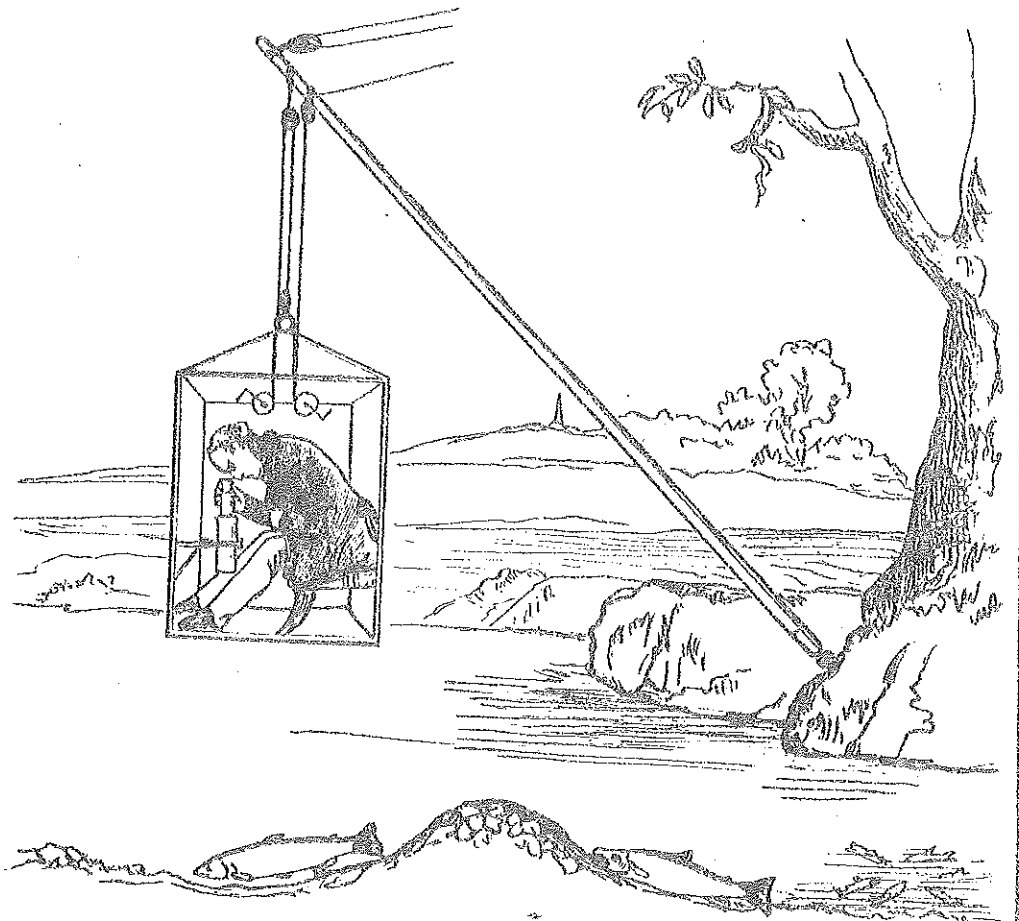## från SÖTVATTENSLABORATORIET, DROTTNINGHOLM

Ömsesidig påverkan mellan fiskarter

av

Nils-Arvid Nilsson.

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Bifogade uppsats är ett föredrag, som hölls vid ett symposium anordnat av Internationella Biologiska Programmets sektion för fiskproduktion i sötvatten i Reading, England, i september 1966. Den är ett försök att sammanfatta erfarenheter om fiskarters ömsesidiga påverkan med tonvikt på vad som i dagligt tal kallas "konkurrens", d.v.s. en process som leder till att båda eller alla agerande arter påverkas ogynnsamt, eller att en art blir allenarådande på de andras bekostnad. Eftersom en sådan process kan åstadkommas både av konkurrens och predation - ibland i kombination - har man stundom känt behov av en term som innefattar hela processen och som antyder att arterna utövar ett "tryck" på varandra. I uppsatsen lanceras termen "interactive segregation", som först användes av engelsmannen Brian (1956), och som tar fasta på det faktum att interagerande arter tvingar varandra att så att säga odla sin egenart. D.v.s. små skillnader i ekologi förstoras då arter som utövar konkurrens eller predation sammanlever. Resultatet blir - för att använda ett klassiskt ekologiskt talesätt - att arterna kommer att leva i var sin ekologiska nisch.

En mängd exempel visar att bakom den segregerande processen förutom predation finns flera olika konkurrensmekanismer. Fenomenet har i uppsatsen (sid. 11) karakteriserats på följande sätt:

1. "Interactive segregation" kan förekomma mellan taxonomiskt vitt skilda arter, men torde vara starkast mellan nära besläktade.

2. Den kan innebära att arterna lever i delvis eller total samexistens. I detta fall återfinns emellertid arterna i olika näringsnischer eller i olika delmiljöer (mikrohabitat).

3. Alternativt kan den innebära att en eller flera arter helt trängs undan eller elimineras.

4. Den upprätthålls genom individernas beteende, d.v.s. fiskarna reagerar på olika stimuli genom att attraheras eller undvika, t.ex. genom närings- eller miljöpreferenser, eller genom aggressivitet eller annan slags negativ påverkan. Små skillnader i, exempelvis, medfödda preferenser för näring eller miljö eller förmågan att

skrämma i form av hotställningar el.dyl. i olika situationer upp-
rätthåller segregationen då resurserna är begränsade.

5. Den varierar tidsmässigt, är mest utpräglad då resurserna är begräns-
ade,mindre utpräglad då resurser finns i överflöd.

6. Eftersom den alltid innebär att arterna delar på tillgängliga re-
surser, kommer den också att innebära att varje art tvingas att i
viss mån specialisera sig och utnyttja en liten men specifik del av
resurserna. På samma gång innebär den emellertid också att resur-
serna blir mer och mer komplett utnyttjade ju flera arter som är
närvarande.

I den praktiska fiskevården är den sista punkten av fundamental
betydelse eftersom den innebär att man aldrig kan rätt bruka ett vat-
ten utan att ha fiskartskombinationen i åtanke. Man torde t.ex. ofta
tvingas att välja mellan arter som är relativt småväxta och lever i
täta bestånd och mera storväxta arter som lämpar sig för sportfiske.
Inplanteringen av sik i norrländska öring-rödingsjöar är ett exempel
på hur en åtgärd, som ur ren produktionssynpunkt på sin tid var riktig,
blir katastrofal då den ses ur sportfiskesynpunkt.

Förutom en allmän insamling av fiskproduktionsdata från olika ty-
per av sjöar världen över med särskild hänsyn till artkombinationen,
föreslås att forskningen i ifrågavarande avseende koncentreras på följ-
ande:

1. Segregationsmekanismer. Etologiska och fysiologiska studier av
attraktiva och undvikande reaktioner. Parallella studier i naturli-
ga vatten och i experimentella anordningar.

2. Detaljerade studier av de processer som igångsätts då nya arter in-
vaderar eller introduceras i ett vatten. Långa serier av provfis-
ken och andra provtagningar före och efter den nya arten har eta-
blerat sig.

3. Liknande studier i samband med total eller partiell förgiftning av
fiskbestånd.

4. Experiment med olika artkombinationer i rotenonbehandlade eller
naturligt fisktomma vatten.

Interactive segregation between fish species   1)
By Nils-Arvid Nilsson

In this paper the term interactive segregation has been chosen
in order to avoid the controversy and semantic discussion that too
often follow the use of the word "competition". The term was first
used by Brian (1956) and means that ecological differences between
species (e.g. in food or habitat selection) are often magnified through
interaction, i.e. the species segregate into different niches through
competition and/or predation. This phenomenon is held to be typical
of "young faunas", e.g. within recently deglaciated areas, where eco-
systems are still in a relatively rapid process of evolution (of.
Dunbar 1960) and presupposes a considerable plasticity in habits as
"optima" or "preferences" change in the presence or absence of inter-
acting species (of. Svärdson 1949, Nilsson 1955, 1963, 1965, Macan
1961). The hypothetical end of the process should be what Brian called
selective segregation, which refers to species that are phylogeneti-
cally distant or else have evolved differences, either incidentally
inallopatry or through reinforcement in sympatry, sufficiently to be
ecologically isolated in the sense of the evolutionists (of. e.g. Mayr
1942, 1963). Selective habitat segregation of fish may mostly be a
matter of temperature preferences or the structure of spawning sites.

Examples of interactive segregation of fish species

Theoretically the populations of most species of fish of the northern
temperate hemisphere should provide examples of interactive segregation,
but although segregation is often easily demonstrated it is more difficult
to prove if it is an immediate result of interaction or of completed
ecological divergence. The view obtained by taking single samples has
often led to the false or at any rate too simple interpretation that the
species either (a) are segregated into different niches and do not
compete or (b) use similar resources and do compete.

The most rewarding situation for the study of the effect of inter-
actions is that of datable changes, for instance the invasion of a new
predator such as the sea lamprey in the Great Lakes (Moffet 1956) or

1) Paper delivered at the IBP Meeting in Reading, England, September 1966.

heavy fishing as in Windermere (Le Cren 1959) and Heming Lake (Lawler 1962) or impoundments (reviews by, e.g., Runnström 1964, Nilsson 1964), or, best of all, the deliberate introduction of new species. One of the best-recorded cases of introduktion is that of Paul Lake in British Columbia (Larkin and Smith 1954, Crossman 1959, Johannes and Larkin 1960), where the introduction of redside shiner, _Richardsonius balteatus_ (Richardson), led to a complicated situation involving competition for food between the introduced species and its predecessor, the rainbow trout, _Salmo gairdneri_ (Richardson), and predation both by redside shiner on rainbow fry and rainbow on adult shiner. During the initial phase both shiner and rainbow fed to a great extent on amphipods, but at the end of the observation period (after about 15 years) the shiner fed mainly on planktonic Crustacea, the rainbow over 30 cm mainly on shiners; and as Johannes and Larkin (1960) remarked: "In recent years amphipods have been scarce in the lake, and have formed only a small fraction of the stomach contents of trout and shiners. On the basis of this observation alone an observer would hardly suspect that amphipods had been the most important item of competition."

Another approach has been to compare the ecology of interacting species when coexisting and when living separately and to study their behaviour. The result of the introduction of arctic char, _Salvelinus alpinus_ L. into pure trout lakes, meaning a decreased growth rate of trout in Norwegian lakes (Dahl 1920, Sømme 1933, Huitfeldt-Kaas 1935, Schmidt-Nielsen 1939, Aass 1960), induced Svärdson (1949) and Nilsson (1955, 1960, 1963, 1965) to study the interaction between the two species. It appeared that when living separately the species have similar food habits but when living sympatrically they are segregated into separate food niches, especially when food is in short supply. It has also been noted that trout regularly spawn both in running water and in the lakes themselves when living in the absence of char (Sømme 1941) whereas in the presence of char they spawn in running water. Moreover, it has been shown (Curry-Lindahl 1957) that char, in parts of the north Swedish highlands where trout are absent, regularly dwell in running water, which is not usually the case where trout is present. In a similar way Lind-roth (1955) demonstrated that juvenile Atlantic salmon and sea trout were segregated into different habitats when living together in a Baltic river, but the Atlantic coast salmon in the absence of trout

preferred a habitat corresponding to the trout habitat in the Baltic river. In that connection Svärdson (1966) has pointed out that land-locked populations of Atlantic salmon are more common at the American eastcoast (where brown trout did not spontaneously occur) than in Europe.

Good examples of the plasticity in habits are provided by the genus *Coregonus*, where the ecological features of species are modi-fied and recombined from lake to lake, probably owing, among other things, to the species combination (Svärdson 1957, Lindström and Nils-son 1962, Nilsson 1960). The differential growth rate might in the case of such closely related species be of fundamental importance for keeping the species populations segregated (Svärdson 1949b). In Vojm-sjön in northern Sweden, for instance, (*C. peled* Gmelin) is a dwarfed plankton- and insect-feeder, *C. pidschian* (Gmelin) a mediumsized bott-bottom-feeder, whereas in Uddjaur-Storavan, where the "plankton niche" is occupied by *C. lavaretus*, *C. peled* is a fast-growing insect-feeder and C. pidschian is still a medium-sized bottom-feeder. The juvenile fish, however, showed no sign of segregation (Lindström and Nilsson 1962). In Algonquin Park in Canada Sandercock (1964) showed that in the presence of *C. clupeaformis* (Mitchill) *Prosopium cylindraceum* (Pallas) has a more restricted habitat and slower growth rate than when *C. clupeaformis* is absent.

Interactive segregation does not occur only between closely re-lated species. Kawanabe (1959) and Miyadi et.al. (1960), for example, showed that *Cobitis biwae* changed its feeding habits and restricted its habitat in the presence of cyprinids, *Pungtungia herzi*, *Hemibarbus longirostris*, or gobiids, *Pseudogobio esocinus*; similarly the cyprinid *Zacco platypus* in the absence of Ayu, *Plecoglossus altilevis*, dwell in the central parts of the rapids and feed on bottom algae, but when the anadromous *Pleocoglossus* ascends the river the cyprinid inhabits more peripheral habitats and feed on terrestrial insects (Miyadi et al. 1952, Kawanabe 1959).

The last example leads us to the idea that interactive segregation may be a matter of seasons or other very temporal processes. Hartman (1965) showed that juvenile coho salmon, *Oncorhyncus kisutch* (Walbaum), and steelhead trout, *Salmo gairdneri* Richardson, occurred together in streams of British Columbia but during spring and summer they had different microhabitats, coho being mainly a pool species, steelhead

mainly confined to riffles. Experiments showed that during that time, however, the two species had very similar demands if they were kept separately. During winter, on the other hand, both species dwelt together in pools, and experiments revealed that their demands were dissimilar and the agonistic motivation was weak. In the case of food habits Nilsson (1960) showed that seasonal fluctuations in the overlap of food niches between brown trout and char were probably the result of superabundance of food or shortage of food, the limits of the niches being broken down when food was superabundant. Gee and Northcote (1962) found that leopard dace, <u>Rhinichthys falcatus</u> (Eigenmann and Eigenmann) and longnose dace, <u>R. cataractae</u> (Valencienne), occurred together as recently emerged fry in summer when food appeared to be superabundant, but were segregated later in summer and autumn when the water of the river receded from the favourable areas. Similarly Keast (1965) showed that in Lake Opinicon, Ontario, periods of greatest food overlap among the fish species usually coincide with peaks of abundance of the various food items.

One of the most drastic examples of removal of resources is the effect of impoundments through large water-level fluctuations. In the Scandinavian subarctic lakes subjected to impoundment, for instance, a very high proportion of the large bottom-dwelling crustaceans (<u>Gammarus lacustris</u> L.) and insect larvae are eliminated and ultimately there is, in the zone of water-level fluctuations, an altered, very sparse bottom fauna consisting of few species (Grimås 1961). In response to this removal of food, brown trout and char become more segregated into different feeding niches than before impoundment, brown trout feeding primarily on terrestrial insects, char primarily on planktonic Crustacea (Nilsson 1960, 1964).

The extreme result of interaction, especially emphasized by experimental workers and entomologists (Gause 1934, Park 1948, Frank 1952, Birch 1954, DeBach and Sundby 1963), is the complete displacement of one or more species through the invasion or introduction of another species. In the case of insects this has been referred to as competitive displacement of ecological homologues (DeBach and Sundby 1963), but in the case of fish in nature it is probable that usually both competition and predation are at work. The displacement can either involve the total elimination of the defeated species, or mean that it is pushed

away to some marginal habitats, where it lives without too much over-
lap in relation to the interacting species. The phenomenon has been
most clearly demonstrated in connection with introductions of exotic
species. The introduction of the European brown trout into North
America, for instance, has in many cases resulted in displacement of
native species (Dymond 1955, Fenderson 1954, Brynildson et al. 1964,
Nelson 1965). In Wisconsin Brynildson et al. noted that in streams
where brown trout were introduced, brook trout, Salvelinus fontinalis
Mitchill, inhabited the cold shallow headwaters, brown trout the
deeper, slower and warmer water downstream, and that in some streams
that were normally occupied by brook trout, the brown trout became
dominant. In Alberta Nelson found it probable that a marked decrease
in the populations of Dolly Varden, Salvelinus malma Walb., brook
trout, cutthroat trout, Salmo clarki Richardson, and rainbow trout,
Salmo gairdneri Richardson, where their ranges overlapped with brown
trout, resulted from interactions from the latter species. The in-
troduction of North American species into Europe, on the other hand,
has on the whole been less successful. For example, in Sweden brook
trout, rainbow trout and largemouth bass, Micropterus salmoides
(Lacépède), were introduced as long ago as the end of the last century,
but these introductions merely resulted in one reproductive population
of rainbow, and reproductive populations of brook trout are, although
more common, scattered in a few cold and narrow source-streams. Vivier
(1955), who listed numerous attempts to acclimatize brook trout and
rainbow in France, noted that they all had been unsuccessful except
in a few isolated places where brown trout were absent. Lake trout,
Salvelinus namaycush Walb., was introduced into Swiss high alpine lakes
in the later part of the nineteenth century, but there seems to be no
certain evidence of any spontaneous reproduction although stocked
fish have appeared to thrive well, judging from their survival and
growth. In one case the presence of alpine char has supposedly de-
pressed the growth of stocked lake trout (Grimås and Nilsson 1962).
Later, lake trout were introduced both in Finland (Sormunen and Kajo-
saari 1963) and Sweden (EIFAC 1964, Svärdson and Nilsson 1964). Be-
ginning in 1957 in Finland and in 1960 in Sweden over 25 Finnish and
55 Swedish lakes have been stocked with that species. In certain
selected lakes the effect of the introductions are carefully studied

by means of test fishing, but so far no reproduction or interaction with native species except predation on whitefish has been recorded. Landlocked sockeye salmon, kokanee, _Oncorhynchus nerka_ Walb., have also been introduced into Swedish lakes without any signs of success-ful reproduction.

In Scandinavia the best-documented example of displacement of species is the introduction of whitefish, _Coregonus_ spp., into many trout-char lakes of northern Sweden. Ekman (1910) listed nine northern Swedish lakes where whitefish had been introduced between the 1820s and the 1870s. In all these cases, as well as in those of more recent introductions, char has either been completely eliminated or has re-mained in small populations. Bad growth and survival of adult char introduced into whitefish lakes has indicated that the interaction does not affect juvenile fish only (Svärdson 1961). Another documented Scandinavian case of displacement is the grayling, _Thymallus thymallus_ L. which in certain circumstances forced brown trout out of its habitat. In Denmark Larsen (1947) reported on an introduction of 16 adult grayling into the River Gudenaa in 1936. This small group gave rise to a large population which after about ten years had obviously de-pressed the native brown trout population.

Mechanisms in interactive segregation

Possible mechanisms working in the segregation process may be (a) _exploitation_, that is, according to Brian, an interaction that may "develop whenever one species is more efficient in a habitat than another, perhaps because it can find and use vacant resources more easi-ly and quickly than the other", (b) _territoriality_, i.e. defence of an area (Noble 1939),(c) _food fighting_, i.e. agonistic activity occur-ring in relation to feeding, (d) _predation_ or (e) other _interference_.

An example of the exploitation type of competition has been described by Johannes and Larkin (1961) when studying the interaction between redside shiner and rainbow. The authors observed that when the two species competed for _Gammarus_, the shiners were quicker to notice the prey and quicker to start feeding than were the trout. They appeared on the whole to feed more efficiently, and they were able to catch the _Gammarus_ deep in the _Chara_ beds where the trout

could not reach them, and at a stage when the trout did not appear to notice them. The end result was that after about 25 years of common exploitation of the Gammarus population the trout had almost stopped feeding on Gammarus, and it is of interest that only occasional contests between shiner and trout were observed although trout often chased and nipped each other.

Ivlev's (1961) very extensive experiments have given much valuable information on how exploitative competition and resulting segregation may work. As regards mixed groups of two species, for instance, he showed that the "ranking" of preferred and avoided food items characteristic of species could be changed by putting competing species together. By means of an "electivity index" he could show that, although all species in his experimental group (carp, goldfish, pumpkinseed and catfish) when kept alone preferred chironomid larvae, when kept in mixed groups they changed their scale of prefence. For instance, goldfish turned to plants in the presence of carp and pumpkinseed, Lepomis gibbosus L., turned to Daphnia in the presence of catfish, Ameiurus sp. Although Ivlev mentions the existence of "mutual scaring, mutual hindrance, reciprocal interference, etc.", and noticed that "predatory species", (Lepomis and Ameiurus) were stronger competitors than were "peaceful species" (carp and goldfish), the predatory species being more fixed to their specific ranking of food types, his results on the whole point more to the action of exploitation than to interference.

It seems to be a presupposition that exploitation should always have an element implying that one species "scrambles" away the resource in question before the other species has tried to use it, either, for instance, because of some sort of physiological timing (e.g. time of sexual maturity) or because it has not learned to use it. This is easiest to imagine, for instance, in the case of one species reaching a certain place (e.g. a spawning area) before another, but could also be imagined in the case of food selection, as slight innate differences in food preference could be magnified in combination with learning (cf. Nilsson 1965). Northcote (1954), in connection with a study of the interrelationships of two cottid species, also pointed out the significance of minor differences in mouth size, stating that such differences may make larger food organisms available sooner to the largemouthed species.

A very well-documented and relatively easily understandable
mechanism in species segregation is territoriality. Several investi-
gations have shown that fighting for territories, although most ob-
vious between members of the same species, also frequently occurs
between species. This can be a case of a territorial fish such as the
Ayu, _Plecoglossus_, chasing away the taxonomically distant cyprinid
Zacco and the goby, _Rhinogobius similis_, (Kawanabe 1959) or closely
related salmonids such as brown trout and Atlantic salmon (Kalleberg
1958), brook trout and rainbow trout (Newman 1956), coho salmon and
steelhead trout (Hartman 1965), which by being similar in behaviour
"understand" one another's threat display.

Newman found that brook trout exhibited more elaborate behaviour
than did rainbow trout under the circumstances studied (in aquaria)
and "they behaved toward each other as though they were one species",
and later when studying the same species under natural conditions
(from a submerged observation tank in a cold alpine stream) he was able
to establish that a mixed group of six trout formed a complete inter-
specific nip-right hierarchy in which status was determined by size
irrespective of species. The hierarchy was maintained by means of
nipping and chasing or a stereotyped threat display comprising fin
erection and lowering of the hyal bones. Rainbow trout was found to
be of a more roaming disposition than brook trout, the latter species
being more strongly territorial and having a more refined threat be-
haviour.

Very similar conditions were reported by Kalleberg in the case
of juvenile salmon and brown trout kept in a large stream tank. The
behaviour analysis revealed that both species, beside nipping and
chasing each other, had an almost identical set of threat displays,
mainly in the form of a frontal display (arched back, dorsal fin
lowered and bottom of mouth "dilated downwards in the shape of a
light-coloured shallow pouch"), and a lateral display (Fabricius 1953)
(stretched back, all fins erected, the bottom of the mouth forming a
Gular pouch). To the last-mentioned display was sometimes added a
violent oscillation of the body and parallel swimming. Under the
conditions existing in the experimental tank, brown trout clearly
dominated over salmon parr of corresponding size.

In neither of the above-mentioned two experiments could it be

established that the mutual agonistic behaviour favoured one species in one particular habitat and another species in another habitat. This, however, was possible for Hartman when studying the behaviour of juvenile coho salmon and steelhead trout in different habitats. Although the two species appeared to have similar sets of aggressive activities, there were slight differences in the frequency. For instance, nipping and chasing were more frequent with trout, whereas lateral threat display and "wig-wag display" (erected fins, inclined posture and accentuated swimming movements) were more frequent with coho. Moreover, trout were significantly more aggressive in riffles, coho more aggressive in pools, and this difference accounted for the segregation of trout and coho in the different habitats. The degree of aggressiveness, however, varied markedly seasonally, being at a low rate in winter, which enabled the two species to coexist in pools during that season.

Several students of fish behaviour have noted that aggressiveness is often accentuated in connection with feeding. This has been found to be true of brook trout and rainbow trout (Newman 1956), of coho salmon and largemouth bass (Mac Phee 1961), Atlantic salmon (Keenleyside and Yamamoto 1962), medaka, Oryzias latipes Temminck and Schlegel (Magnuson 1962), and of young brown trout and arctic char (Nilsson 1963, 1965). The degree of aggressiveness seems to be inversely proportional to the supply of food; that is to say, a superabundance of food weakens aggressiveness. In the case of nipping and biting it seems obvious that feeding could very easily be transformed into aggressive behaviour. Kalleberg (1958) has, however, also pointed out that there is an extraordinarily great similarity between the frontal threat display of young salmon and trout and their behaviour when swimming towards a prey situated on the bottom.

In the case of medaka and juvenile arctic char aggressiveness seems to be linked exclusively with feeding, and, as Magnuson stated, aggressive behaviour in such cases is not used in competition for space per se but is a mechanism that reserves a greater portion of a limited food supply. When forced to coexist with brown trout in a trough or tank, young char compete successfully with that species (Svärdson 1949), also in the form of the char showing aggressive behaviour against the trout (Nilsson 1965). It may in this connection be mentioned that junvenile brown trout and

char would hardly be found together in nature, as when living sympatrically the young fish are strongly segregated, the trout in running water, the char in deep water in the lake itself. There do not seem to be any records of interspecific food fighting in nature between fish, and it would certainly be difficult to trace. If it did exist it would be of great importance in species segregation and food competition.

The role of predation in species segregation is obvious and has been dealt with in another section of this Symposium. It involves both segregation, as the prey in balanced systems possess mechanisms for escape, and coexistence, especially as most balanced predator-prey systems are "buffered", that is to say, the prey has a "maximum safe density", when "predators no longer find it sufficiently rewarding to forage for them" (Ricker 1954). Differential ability, especially of young fish of different species, to avoid predators in different situations, may also reinforce segregation of sympatric prey species.

The enormous effect that can be brought about by the invasion of a new predator, has been illustrated by the history of the lamprey invasion into the Great Lakes. On the other hand many Swedish experiences of incomplete treatments with rotenone have indicated that the removal of predators such as the pike can give rise to large populations of species that before the treatment were rarely caught. Many interactive processes, however, are probably complicated combinations of predation and competition like that between redside shiner and rainbow trout in Paul Lake. In this context one should be especially aware of the complications that the coexistence of many different age groups may involve. For example, Le Cren (1962), when estimating the consumption of food by pike of different ages, found that the pike population as a whole may consume as much plankton as do other fish with less general predatory habits.

Finally, it should be added that other segregating mechanisms than those treated so far could be imagined to exist. Ivlev described an experiment where he had equipped aquaria with screens (transparent and opaque) that divided the aquaria into intercommunicating sectors. When keeping mixed groups of fish of different species in the aquaria he found that there was a tendency for only one species of fish to occur in each sector. The experimental fishes were all of species lacking aggressive behaviour in the proper sense of that term. Of great interest in this connection are Gudger's (1929)[x] observations

x) quoted by Breder (1929)

that alien species passing through shoals of _Jenkinsia stolifera_ caused "empty spaces" around themselves, i.e. _Jenkinsia_ individuals avoided approaching the strangers. These observations may point to the possibility that interspecific avoidance could be released by other stimuli than threats or attacks, for example by strange sizes, colours, movements, sounds or odours. Also the possibility of direct changes of the environment through the action of certain fish species may in this context be mentioned. The European carp, for instance, introduced into North America during the 1880's and since then looked upon as being adverse to other fish species such as the buffalo (_Ictiobus_ sp.) (Carlander 1954), seems to have acted partly through increasing turbidity and eliminating vegetation (Cahn 1929, Threinen and Helm 1954).

Characteristics of interactive segregation

Summing up the foregoing examples, the following characteristics of interactive segregation may be discerned:

(1) Interactive segregation can occur between taxonomically distant species, but may be most severe between closely related species.

(2) It can imply total or partial coexistence, in which case, however, the species will be segregated into different food niches or microhabitats.

(3) Alternatively, it can imply total displacement or exclusion of one or more species.

(4) It is governed by behaviour, that is to say, the fish respond to stimuli of attraction or avoidance, such as food or habitat preferences, conditioning, and threats or other interference. Slight differences in, for instance, innate preferences or ability to threaten in different situations maintain segregation when resources are limited.

(5) It varies temporarily, being pronounced when resources are limited and less pronounced or non-existent when resources are superabundant.

(6) As it always means a sharing of resources, it will mean that a given species with a broad ecological potency is forced, so to speak, to realize its specific qualities, taking a smaller but more specific share of the resources. At the same time, however, the resources should be more and more

completely exploited the more species are present to exploit them in their own specific ways.

Comments

The last point brings us to the essential problem of interactive segregation in regard to this Symposium. The contention was, basically formulated as follows by Carlander (1955) after having analysed the standing crops of a great number of North American ponds, lakes and reservoirs: (Analyses indicate) "an increase in the standing crop of a body of water as the number of species of fish increases, but maximum crops of selected species in lakes or ponds with not more than one other species." To test whether this phenomenon is a result of competition, Carlander also measured the regressions of standing crops of given species in relation to other species, negative regression determining a possible effect of competition. As might be expected, he found such an effect between species of approximately the same trophic level. Thus, for instance, there was a negative regression between bluegill, *Lepomis macrochirus* Rafinesque, and green sunfish, *L. cyanellus* Rafinesque, bluegill and bullhead (*Ictalurus sp.*), white crappie, *Pomoxis annularis* Rafinesque and black crappie, *P. nigromaculatus* LeSueur, and between carp, *Cyprinus carpio* L. and buffalo, *Ictiobus* sp.. There was, however, a similar effect also with species with differing food levels, such as largemouth bass and bullhead, largemouth bass and carp, and largemouth bass and gizzard shad, *Dorosoma cepedianum* (LeSueur). It is noteworthy that in some cases there were significantly positive regressions, e.g. between largemouth bass and various forage fish species.

The last example serves to indicate the validity of what supposedly most fishery managers have as a guiding principle when stocking their waters: that the ideal fish combination is predator plus prey, or else species of different trophic levels such as bottom-feeders plus plankton-feeders, etc. Several of the above examples, however, including that from Paul Lake, indicate that this is not a universal rule.

The maximum standing crops of many of the ponds examined by Carlander (*op.cit.*, p. 559) reached their maximum values when two species were combined. This supports the general idea that temperate fish species "have generalized feeding habits and relatively wide tolerance of habitat" (Larkin 1956), which may mean that the available niches of

a water are relatively easily "filled" by just a small number of
species. This also means that the more species are present, the more
difficult it will be to establish populations of new species.

It is, and will still be difficult to form general rules for
fishery management in regard to the present theme. To take an example,
the fishery of the north Swedish highlands has developed (typically)
from primitive hook-fishing for native species via a more planned net-
fishing combined with stocking of new species with dense populations
(mainly whitefish) to a recreational fishing for game fish by tourists.
The esteemed species are again the indigenous ones, and it is easy to
imagine that such changes, and corresponding geographical variations
must result in very varied objectives for management. The managers who,
for instance, stocked the Swedish trout waters with whitefish, thus in-
creasing the protein production, could hardly anticipate that this some
decades later would be looked upon as a severe harm to the sport fishery.
Generally it seems that most fishery managers by necessity should have
to choose between species with short food chains and dense populations
(used as food) and carefully selected game species, that should pre-
ferably not interact adversely on each other. A worldwide collection
of data corresponding to those published by Carlander would be of great
help in planning inland fishery management in regard to interspecific
interactions. In the long run, however, we cannot even be satisfied
with just measuring standing crops, as rarely they are directly proportional to
production. One, as I imagine, rather realistic possibility to study
fish production in relation to interspecies interaction, would be to
measure the number of migrating individuals of anadromous fish (in
different species combinations) by means of traps in running water.

Mathematical analysis like that of Larkin (1963) are also very
valuable for clarifying our thoughts, but I think we have to admit
that there is a very broad gap between available data and theory. For
the rest it seems to me that research on interspecific relations should
concentrate on the following themes:

1. Mechanisms in segregation; behaviour and physiology in regard
   to attractions and avoidance. Parallel studies in natural wa-
   ters and experimental tanks, fluviaria (Höglund 1961), etc.
2. Detailed studies of processes brought about by invasions or
   introductions of new species. Long series of test fishing

operations and sampling before and after the establishment of
the new species.

3. Similar collections of data in connection with total or partial
poisoning of fish populations.

4. Experiments with different species combinations in reclaimed
waters.

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