

Dr. Tyler,

Belinke

Please return

Thanks

Dennis-

Effects of streamflow and upwelling on abundance
of wild coho salmon (Oncorhynchus kisutch) in Oregon.

Dennis L. Scarnecchia¹

Oregon Cooperative Fishery Research Unit²

Oregon State University

Corvallis, Oregon 97331

¹Present address: Colorado Cooperative Fishery Research Unit, Colorado State University, Fort Collins, Colorado 80523

²Cooperators are the Oregon Department of Fish and Wildlife, U. S. Fish and Wildlife Service, and Oregon State University.

ABSTRACT

To investigate the relation between both streamflow and upwelling and abundance of coho salmon (Oncorhynchus kisutch), I examined the correlation between flows from five Oregon coastal rivers, as well as upwelling at two offshore locations, and catch of coho salmon by the Oregon commercial troll fishery. A highly significant relation was found between total streamflows during the freshwater residency of the fish for the five rivers combined and kilograms of adult coho salmon caught by the fishery from 1942 to 1962. There was also a significant relation between total combined annual (January-December) flows for these rivers and the catch 2 years later. Conversely, I found a poor relationship between the 60 consecutive days of lowest flow during summer and catch 2 years later. Higher flows during the freshwater stages of coho salmon probably provide more habitat and better conditions for growth and survival.

I also found a significant relation between combined April through June upwelling at both stations and catch of coho salmon one year later from 1947 to 1962. Fifty-six percent of the variation in catch from 1947 to 1962 was explained by the total flows during freshwater residency, 60 consecutive days of lowest flow, plus combined April through June upwelling at both stations.

It is suggested, contrary to some hypotheses, that some coho salmon smolts may move southward or remain stationary offshore following entrance into the ocean, to utilize increased production of invertebrates that result from upwelling.

I advise caution in using the model to predict current abundance of wild salmon, because of potential interaction of wild and hatchery-reared salmon, possible changes in the oceanic environment since 1962 or possible insufficient escapement. More study is needed on ecology of coho salmon in the ocean.

Key Words: streamflow, upwelling, coho salmon, Oregon coast.

INTRODUCTION

Yearly abundance of coho salmon (Oncorhynchus kisutch) has historically fluctuated widely, causing economic problems for commercial fishermen and management problems for fishery biologists. Ability to predict coho salmon abundance before the fishing season enables fishermen to allocate time and money efficiently and allows biologists to recommend harvest rates that will prevent overfishing of stocks.

Inasmuch as catches of coho salmon on different rivers tend to fluctuate together (McKernan et al. 1950, Tollefson 1959), biologists have searched for widespread environmental factors influencing abundance. One approach to predicting abundance well before the fishing season has been to correlate large-scale environmental variables with the catch of adult coho salmon by either the terminal fisheries (such as gillnet and dipnet) or troll fisheries. Neave (1949) reported a significant correlation between number of coho salmon caught per 100 h or sport fishing in Cowichan Bay, British Columbia, and minimum summer streamflows 2 years earlier;³ and Smoker (1955) found

³Most coho salmon contributing to fisheries are age 1.1 where number left and right of the decimal indicate number of marine and freshwater annuli on their scales, respectively. If coho salmon are caught as age 1.1 adults in year x, they were fry in streams in year x-2 and yearling in year x-1. Their parents probably spawned from about November, x-3, to January, year x-2.

the combined annual runoff from 21 watersheds in western Washington highly correlated with total combined catch of coho salmon 2 years later by the commercial fisheries of Puget Sound, Willapa Bay, and Gray's Harbor. Smoker also

obtained significant correlations between summer flow, as well as lowest monthly flow, and catch 2 years later. He concluded that these flows merely reflected annual flows. Summer flow was influenced by melting of snow and glaciers. He was unable, however, to show significant correlations between streamflow and catch for most individual rivers. The Washington Department of Fisheries now estimates number of wild coho salmon returning to Puget Sound streams by using summer streamflows of western Washington 2 years before the catch (Zillges 1977).

It has been assumed that available rearing area during low summer flows limits most coho salmon populations in Washington. However, Wood⁴ found

⁴Wood, W. 1977. Methods of estimating escapement requirements, preseason run size, and in-season run size of north coastal salmon stocks. Washington Department of Fisheries. 7 pp.

poor correlations between low summer flows of western Washington coastal streams and the size of the ensuing runs, as determined from gillnet catches. He suggested that other factors, singly or in combination, may dictate the number of adults produced.

Factors in freshwater other than summer flows affect smolt output and resultant return of adults. Predation acting on fry each year from the end of summer until seaward migration affects the return of adult fish. Elson (1962) found that the survival of Atlantic salmon (Salmo salar) smolts increased by controlling merganser populations. Variable predation would lead to significant variability in number of smolts entering the ocean each year.

High, though not torrential, flows from March through May, the usual time of downstream migration for smolts, could lead to increased growth and decreased predation because of increased turbidity of the water and accompanying available feeding opportunity and cover.

High streamflows when adult spawners are entering rivers may allow access to upper spawning areas that are inaccessible during lower flows, leading to production of smolts in upper tributaries (Allen 1969). Higher flows may also increase the area of spawning beds. Of course, fish spawning in gravel inundated by high flows may die if flows drop before fry emerge.

In the present study, I investigated certain relationships between streamflows of coastal Oregon rivers and yield of adult coho salmon to the offshore commercial troll fishery. My objectives were to (1) investigate the correlation between low summer streamflows and coho salmon catch 2 years later, (2) investigate the correlation between annual streamflows as well as total flows during the freshwater phase of the juvenile life of coho salmon and catch of adult fish subjected to these flows as juveniles, (3) compare results from (1) and (2) with those of Smoker (1955) to determine whether summer streamflows are correlated better with catch than annual streamflows, (4) investigate the correlation between peak discharge of rivers and catch of coho salmon subjected to those flows as juveniles, (5) investigate the correlation between flows during spawning migrations and the catch of coho salmon 3 years later, and (6) investigate the correlation between post-summer flows (i.e. those of winter and spring as well as those during time of smolting) and catch of adult coho salmon.

Little is known about how variable oceanic factors affect survival of coho salmon from smoltification to maturity. Royal and Tully (1961) found that

marine survival rates of sockeye salmon (Oncorhynchus nerka) ranged from 4 to 18 percent over several years.

Upwelling is one oceanic factor which may affect survival of coho salmon. Bakun (1973) described upwelling as "the replacement from below of surface waters transported offshore by stress of wind on the sea surface". The process occurs on a large scale at several locations around the world (e.g. off of western South America and western Africa) and is often associated with slow-moving eastern boundary currents (Cushing, 1971). Upwelling occurs off of Oregon primarily from April to September, and results from northerly winds blowing down the coast as they circulate clockwise around the large high-pressure system over the Pacific ocean (Smith, et al. 1966, Cushing, 1971, Bakun, 1973). During this time, cold, nutrient-rich, high-salinity water (Lynn, 1967) is transported upward where nutrients are utilized for primary production. The lower temperatures and increase in primary production lead to an increase in the standing crop of zooplankton (Murphy, 1961) which is utilized by many species of commercially important fish. Ryther (1969) has suggested that upwelling areas, while comprising 0.1 percent of the ocean surface, may produce 50 percent of the world's harvestable fish supply.

Upwelling affects the distribution and abundance of many fishes and marine mammals. Townsend (1935, reviewed in Cushing, 1975) found distribution of sperm whales (Cetacea: Physeter catadon) coincided with areas of upwelling. Sardines (Sardinops sagax) and anchovies (Engraulis mordax) utilize upwelled water for spawning and rearing (Ahlstrom, 1966, 1967, Cushing, 1971). Hayman and Tyler (1980) found higher upwelling increased cohort strength of English sole (Paraphrys vetulus) and negatively affected

cohort strength of Dover sole (Microstomus pacificus). Pacific hake (Merluccius productus) may move northward during spring and summer in response to northward shifting of upwelling (Alverson and Larkins, 1969).

For coho salmon, I postulated that if upwelling affects survival, it would exert this effect primarily upon smolts, and not larger salmon, since Gunsolus⁵ showed that survival of Oregon's coho salmon during their final

⁵Gunsolus, R. T. 1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Oregon Department of Fish and Wildlife. Unpublished. 59 pp.

year in the ocean is fairly constant.

Prior to and upon reaching the ocean, the smolts adjust physiologically and behaviorally and begin feeding on pelagic invertebrates. Since coho salmon in Oregon emigrate from streams in April (Skeesick 1970) and May⁶,

⁶Willis, R. A. 1962. Gnat Creek weir studies. Oregon Fisheries Commission. Unpublished. 71 pp.

I postulated that May through July was the critical period for marine survival of coho salmon smolts.

Assuming a lag of 20 to 30 days (Cushing, 1971) between beginning of upwelling and effective grazing by pelagic invertebrates and another lag of 10 to 20 days for increased production and standing crop, I first hypothesized that higher upwelling from April through June would positively

affect survival of coho salmon smolts and lead to a high abundance of adult fish the following year. Secondly, this upwelling during early summer, although lower in magnitude than midsummer upwelling (June-September), was hypothesized to be more important in affecting coho salmon abundance than the latter. My next objective was to test these two hypotheses.

To develop a model for predicting abundance of wild coho salmon, my final objective was to relate the combined effects of streamflows and coastal oceanic upwelling to subsequent catch of adult coho salmon by the offshore fishery.

MATERIALS AND METHODS

Streamflow data for five coastal rivers--the Nehalem, Wilson, Siletz, Alsea, and Coquille--were obtained from U. S. Geological Survey reports for Oregon (1939-1970; 1971-1973). These reports summarize mean daily discharge at gauging stations along each river. I also secured data on daily discharge on computer cards for these rivers from the U. S. Geological Survey office in Portland, Oregon. These rivers were selected for study for three reasons: data on daily streamflow were available on each river since 1939, records of catch of coho salmon by the offshore fishery were recorded when corresponding data on streamflow were recorded, and the rivers historically have supported substantial populations of coho salmon.

To quantify yearly differences in streamflows during the summer, I developed a computer program to calculate the 60 consecutive days of lowest flow in each of the rivers. Sixty consecutive days of lowest flow are indicative of low flow conditions during each summer. The use of the 60 consecutive days of lowest flow is preferable to the use of average monthly

flows because summer freshets in coastal Oregon rivers seriously bias average values. All flows were expressed as cubic meters per second.

The correlation between catch of coho salmon by the troll fishery and streamflows of Oregon coastal rivers was examined by combining streamflow measurement of the five rivers named above and plotting these combined values for various time intervals against the troll catch from 1942 to 1962. This period was chosen because streamflow data for the years before 1939 were unavailable for two of the five rivers, and the period preceded the years of large returns of hatchery fish to the Columbia River (Korn 1977).

Upwelling data from 42°N, 125°W, off of southern Oregon, and from 45°N, 125°W, off of northern Oregon, were obtained from Bakun (1973). The indices are based upon monthly means of atmospheric pressure fields from which winds and resultant upwelling were estimated. Upwelling is expressed as kg/sec/100 m of coastline. Data were available at both stations before 1946, so multiple regressions with streamflows began with that year.

you did not estimate abundance

For the estimate of abundance, kilograms rather than numbers of fish caught were used because numbers of fish were not recorded before 1952. From 1952 to 1962, numbers and kilograms were closely correlated ($r = 0.98$).

I performed linear and multiple regression analyses on catch, flow, and upwelling data using the Statistical Interactive Programming System (SIPS) of the CDC 3300 computer at Oregon State University, Corvallis.

RESULTS

A significant relation was found between total November (x-3) through May (x-1) streamflows for the five coastal rivers combined and kilograms of coho salmon caught by the Oregon commercial troll fishery in year x

from 1942 to 1962 ($\underline{r} = 0.68$, $\underline{p} < .01$; Fig. 1). This 17-month period of streamflow, from November to May 2 years later, corresponds to the time from entrance of adult salmon to coastal rivers to the seaward migration of their progeny as smolts (Willis 1962⁷, Moring and Lantz 1975). There was also

⁷Willis, op. cit.

a highly significant relation between total annual flow and catch 2 years later ($\underline{r} = 0.56$, $\underline{p} < .01$; Fig. 2). The 60 consecutive days of lowest flow for the five Oregon rivers combined correlated poorly with annual flows ($\underline{r} = 0.20$; $\underline{p} > .05$) and with November (x-3) through May (x-1) flows ($\underline{r} = 0.13$; $\underline{p} > .05$).

Though a highly significant relation between annual flows with catch 2 years later was found, there was a poor relation between the 60 consecutive days of lowest flow and catch 2 years later ($\underline{r} = 0.28$, $\underline{p} > .05$; Fig. 3).

I also found significant relations between catch and (a) total flows from November (x-2) through May (x-1), corresponding to winter and spring flows for the yearlings ($\underline{r} = 0.59$; $\underline{p} < .01$; Fig. 4); (b) total flows from March (x-1) through May (x-1), corresponding to time of smolting ($\underline{r} = 0.53$; $\underline{p} < .05$; Fig. 5); and (c) total flows from January (x-2) through September (x-2), from the time before emergence of the fry until the end of summer ($\underline{r} = 0.44$, $\underline{p} < .05$).

There was no tendency for years of high river discharges to be followed by years when the return of adults subjected to these flows as juveniles was low ($\underline{r} = 0.19$, $\underline{p} > .05$), nor was there any indication that extremely

high flows during spawning of fish influenced catch 3 years later ($\underline{r} = 0.01$; $\underline{p} > .05$).

A significant relation was found between combined April (x-1) through June (x-1) upwelling at both stations and catch from 1947 to 1962 ($\underline{r} = 0.58$, $\underline{p} < .05$; Fig. 6). Similar significant relations were also found between catch and upwelling at each station separately ($\underline{r} = 0.57$; $\underline{p} < .05$ for 42°N 125°W; $\underline{r} = 0.54$; $\underline{p} < .05$; for 45°N, 125°W). Midsummer upwelling (June-September) did not significantly relate to catch ($\underline{r} = 0.34$; $\underline{p} > .05$).

Since total November (x-3) through May (x-1) flows and 60 consecutive days of lowest flow were poorly correlated, I calculated a multiple regression of these flows and upwelling versus the catch from 1947 to 1962. Fifty-six percent of the variation in catch was explained by the flow values plus combined April through June upwelling at both stations (Figure 7). The multiple regression equation was found to be:

$$\text{Catch (x } 10^{-3}\text{)} = -1853.0589 + 0.1499 \times 10^{-6} (\text{total flow}) \\ + 0.3823 (\text{low flow}) + .00109 (\text{upwelling})$$

Sixty-four percent of the variation in catch was explained by excluding data for 1960, the lowest recorded catch, from the analysis.

DISCUSSION

The relation between total annual flows and catch of coho salmon 2 years later is noteworthy, since Smoker (1955) found a similar relation between annual flows and catch of coho salmon in western Washington from 1935 to 1954, an overlapping but not identical time span. I hypothesize that before the years when large numbers of smolts were released from

hatcheries, quantity of streamflow, reflecting quantity and partly the "quality" of freshwater habitat, partially determined abundance of coho salmon.

For Oregon coastal rivers, summer streamflows were not related to annual flows, although Smoker (1955) found a close relation between them in Washington. This difference between Oregon and Washington streams is probably a result of a difference in timing of runoff. The watersheds analyzed by Smoker were fed by melting snow and glaciers in summer, and high precipitation in winter often led to high streamflows the following summer, whereas the five Oregon rivers that I studied flow out of the Coast Range mountains, which receive nearly all precipitation in winter as rain. In these rivers, summer flows are mainly dependent on quantity of precipitation in summer. Although Smoker (1955) found highly significant relationships between both annual streamflow and catch and summer streamflow and catch, he was unable to clearly separate their effects, because total and summer streamflows were closely correlated.

Chapman (1966) noted that size of territories of juvenile coho salmon decreased when abundance of food increased. Higher flows and resultant higher velocities can lead to smaller territories of individual Atlantic salmon (Kalleberg, 1958). Consequently, higher flows during time of emergence through the summer may lead to more space, more cover, more drift of food organisms, and, in turn, to a greater number and density of young salmon in streams. The number of juveniles surviving low summer flows may depend upon their initial numbers. In years of a high number of fry before the period of low flow, more fish may survive the low flows, although their individual

size may be less than in years of low numbers.⁸

⁸Pearson, L. S., K. R. Conover, and R. E. Sams. Factors affecting the natural rearing of juvenile coho salmon during the summer low flow season. Oregon Fish Commission. Unpublished.

Although low summer streamflows are used to predict abundance of wild coho salmon in streams flowing into Puget Sound (Zillges 1977), there is no indication that the correlation between catch and lowest summer flow is, or ever was, high enough in Oregon to allow prediction of coho salmon return to its troll fishery.

After the period of low summer flows, higher flows from November to May generally led to higher catches (Fig. 4). Higher flows in winter may provide more overwintering habitat for fish. High flows in later winter and spring may dislodge invertebrates from the substrate and increase their availability to fish as food. Increased food might then enhance growth and survival of yearlings. These larger smolts would probably have higher rates of return than smaller smolts (Hager and Noble 1976; Bilton and Jenkinson 1977). Additionally, high flows during March through May (Fig. 5) may protect smolts from excessive predation during downstream migration.

From 1963 to 1972, the correlation between total annual flows and catch by the troll fishery was poor ($r = 0.24$, $p > .05$), as expected. During this period, hatchery fish were contributing significantly to the fishery, as indicated by returns of salmon to the Columbia River hatcheries (Korn 1977). Since hatchery fish are not reared in streams, other factors probably affect

their return, e.g. oceanic factors, diseases, or the "quality" of smolts released (expressed as potential for growth and survival in the ocean).

Based upon the above significant relation between upwelling and catch, I believe marine factors also have a significant effect on coho salmon abundance. More study is needed on the biology of salmon in the ocean.

For example, little is known about oceanic movements of coho salmon smolts. Loeffel and Forster (1970) corroborated the hypothesis of northward movement along the coast during summer. However, if upwelling affects survival of coho salmon, then many smolts may also move southward or remain stationary off the coast to utilize available food. This hypothesis should be investigated.

More study is also needed on oceanic feeding habits of coho salmon during their first year and the relation between food supply, upwelling, and survival of smolts. Upwelling may increase production of smaller invertebrates, and thereby increase growth and survival and distribution of larval fishes and larger invertebrates, which may also serve as food for smolts. A causal link must be established between response of food organisms to upwelling and response of salmon to food organisms.

At present, I can only speculate why upwelling may influence survival of year classes of coho salmon. It seems unlikely that smolts would die of starvation in years of little upwelling. Perhaps in these years growth is reduced because of scarcity of food. Smaller, slower-growing smolts may remain susceptible to predation longer than larger smolts. Larger, faster-growing fish with a greater supply of food may resist diseases better than poorly-fed fish. Availability of abundant food may be crucial for growth

and survival following the physiological adjustments coho salmon undergo during smoltification.

It is unknown why the very low catch during 1960 did not fit the model closely. Perhaps the low catch of that year indicated overharvest of the extremely abundant 1957 year class (Fig. 7).

Although catch may poorly indicate abundance of adult fish, the troll fishery is the most reliable source of data on abundance available for comparisons with flow. Since this fishery gets the first opportunity to catch migrating coho salmon and has been virtually unregulated since its inception (Van Hying 1951, Reed⁹), catch is probably more indicative of actual

⁹Reed, P. H. 1976. A history and current status of Oregon ocean salmon fisheries--troll salmon investigations. Oregon Department of Fish and Wildlife. 20 pp.

abundance than data from individual rivers.

I advise caution in using these findings predictively. Since the mid-1960's hatchery fish have comprised a substantial percentage of coho salmon caught offshore (Korn, 1977). Scarnecchia and Wagner (1980) estimated that approximately 75 percent of the coho salmon caught offshore in 1977 were reared in hatcheries. The unknown interaction between the wild and hatchery fish may alter the relationship presented. Other oceanographic factors may have changed since then. Present escapement of coho salmon may be inadequate because of heavy fishing pressure in recent years. For safety, biologists predicting current abundance of wild fish using these methods should consider the derived estimates to be maximum values. If possible, the relationship should be tested with more recent data.

In the past, biologists have often assumed oceanic effects to be constant because investigation of salmon in the ocean is difficult and expensive. Yet oceanic factors may be important or dominant in determining abundance of coho salmon. To adequately understand population dynamics of salmon, biologists must learn more about salmon in the marine environment.

ACKNOWLEDGEMENTS

I thank J. Lichatowich, H. H. Wagner, W. A. Smoker, W. J. McConnell, E. P. Bergersen, C. A. Carlson, J. D. McIntyre, J. D. Hall and others for offering valuable comments, and Clyde Alexander of the U. S. Geological Survey for providing data on streamflows. My special thanks to S. L. Allen for editorial assistance.

LITERATURE CITED

- Ahlstrom, E. H. 1966. Distribution and abundance of sardine and anchovy larvae in the California current region off California and Baja California, 1951-64: a summary. U. S. Fish and Wildlife Service, Special Scientific Reports-Fisheries 534. 71 pp.
- Ahlstrom, E. H. 1967. Co-occurrences of sardine and anchovy larvae in the California current region off California and Baja California. California Marine Research Committee, California Cooperative Fisheries Investigations Report. 11:117-135.
- Allen, K. R. 1969. Limitations on production of salmonid populations in streams. Pages 3-18 in T. G. Northcote, ed. Symposium on Salmon and Trout in Streams. H. R. MacMillan lectures in fisheries. University of British Columbia. Vancouver, British Columbia.
- Alverson, D. L. and H. A. Larkins. 1969. Status of knowledge of the Pacific hake resource. California Marine Research Committee, California Cooperative Fisheries Investigations Report. 13:24-31.
- Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. National Oceanic and Atmospheric Administration Technical Report SSRF-671. 103 pp.
- Bilton, H. T. and D. W. Jenkinson. 1977. The scale characters of jack and adult coho salmon (Oncorhynchus kisutch) which returned from three releases made at Rosewall Creek in April, May, and June 1973. Canada Fisheries and Marine Service Technical Report 715. 19 pp.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist. 100:345-357.

- Cushing, D. H. 1971. Upwelling and the production of fish. *Advances in Marine Biology*. 9:255-334.
- Cushing D. H. 1975. *Marine ecology and fisheries*. Cambridge University Press. 277 pp.
- Elson, P. F. 1962. Predator-prey relationships between fish eating birds and Atlantic salmon. *Fisheries Research Board of Canada Bulletin* 133. 87 pp.
- Hager, R. C. and R. E. Noble. 1976. Relation of size at release of hatchery reared coho salmon to age, size, and sex composition of returning adults. *The Progressive Fish-Culturist*. 38:144-147.
- Hayman, R. A., and A. V. Tyler. 1980. Environment and cohort strength of Dover sole and English sole. *Transactions of the American Fisheries Society*. 109:54-70.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar, L. and S. trutta, L.). Institute of Freshwater Research Drottningholm Report. 39:55-98.
- Korn, L. 1977. Information on Columbia River salmon runs and fisheries. *International North Pacific Fisheries Commission Bulletin*. 36:1-14.
- Loeffel, R. E., and W. O. Forster. 1970. Determination of movement and identity of stocks of coho salmon in the ocean using the radionuclide zinc-65. *Fish Commission of Oregon Research Reports*. 2(1):1-13.
- Lynn, R. J. 1967. Seasonal variation of temperature and salinity at 10 meters in the California current. *California Marine Research Committee, California Cooperative Fisheries Investigations Report*. 11:157-174.

- McKernan, D. L., D. R. Johnson and J. I. Hodges. 1950. Some factors influencing trends of salmon populations in Oregon. Transactions of the North American Wildlife Conference. 15:427-449.
- Moring, J. R. and R. L. Lantz. 1975. The Alsea Watershed study: effects of logging on the aquatic resources of three headwater streams of the Alsea River Oregon. Part one - biological studies. Oregon Department of Fish and Wildlife Fisheries Research Report 9. 66 pp.
- Murphy, G. I. 1961. Oceanography and variations in the Pacific sardine population. California Marine Research Committee, California Cooperative Fisheries Investigations Report. 8:55-64.
- Neave, F. 1949. Game fish populations in the Cowichan River. Fisheries Research Board of Canada Bulletin 84. 32 pp.
- Royal, L. A., and J. P. Tully. 1961. Relationship of variable oceanographic factors to migration and survival of Fraser River salmon. California Marine Research Committee, California Cooperative Fisheries Investigations Report. 8:65-68.
- Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science. 166:72-76.
- Scarnecchia, D. L., and H. H. Wagner. 1980. Contribution of wild and hatchery-reared coho salmon, Oncorhynchus kisutch, to the Oregon ocean sport fishery. Fishery Bulletin. 77(3):617-623.
- Skeesick, D. G. 1970. The fall immigration of juvenile coho salmon into a small tributary. Fish Commission of Oregon Research Reports. 2:1-6.
- Smith, R. L., J. G. Pattullo, and R. K. Lane. 1966. An investigation of the early stage of upwelling along the Oregon coast. Journal of Geophysical Research. 71(4):1135-1140.

- Smoker, W. A. 1955. Effects of streamflow on silver salmon production in western Washington. Ph.D. Thesis. University of Washington, Seattle. 175 pp.
- Tollefson, R. 1959. A summary of fishery statistics of the Pacific coast. Northwest Pulp and Paper Association. 182 pp.
- Townsend, C. H. 1935. The distribution of certain whales as shown by the log book records of American whale ships. *Zoologica*. 19:1-50.
- U. S. Geological Survey. 1939-1970. Water Supply papers No. 884, 904, 934, 964, 984, 1014, 1044, 1064, 1094, 1124, 1154, 1184, 1218, 1248, 1288, 1348, 1398, 1448, 1518, 1568, 1638, 1718, 1935, 2135. Washington, D.C. Superintendent of Documents.
- U. S. Geological Survey. 1971-1973. Water Resources data for Oregon. Washington, D.C. Superintendent of Documents.
- Van Hying, J. M. 1951. The ocean salmon troll fishery of Oregon. Oregon Fish Commission Contribution. 15:46-76.
- Zillges, G. 1977. Methodology for determining Puget Sound coho escapement goals, escapement estimates, 1977 pre-season run size prediction and inseason run assessment. Washington Department of Fisheries Technical Report 28. 65 pp.

LIST OF FIGURES

Figure

- 1 Total November (x-3) through May (x-1) flows ($\times 10^9 \text{ m}^3/\text{sec}$) for five coastal rivers combined versus kilograms ($\times 10^6$) of coho salmon caught in year x by the Oregon commercial troll fishery. Catch data extend from 1942 to 1962. $\text{Catch} (\times 10^{-3}) = -894.5236 + 0.1256 (\text{flow}) (\times 10^{-6})$.
- 2 Total annual flows ($\times 10^9 \text{ m}^3/\text{sec}$) for five coastal rivers combined versus kilograms ($\times 10^6$) of coho salmon caught two years later by the Oregon commercial troll fishery. Catch data extend from 1942 to 1962. $\text{Catch} (\times 10^{-3}) = -176.4991 + 0.1395 (\text{flow}) (\times 10^{-6})$.
- 3 Lowest sixty consecutive days of flow ($\times 10^2 \text{ m}^3/\text{sec}$) for five coastal rivers combined versus kilograms ($\times 10^6$) of coho salmon caught two years later by the Oregon commercial troll fishery. Catch data extend from 1942 to 1962. $\text{Catch} (\times 10^{-3}) = 404.7097 + 0.4557 (\text{flow})$.
- 4 Total November (x-2) through May (x-1) flows ($\times 10^9 \text{ m}^3/\text{sec}$) for five coastal rivers combined versus kilograms ($\times 10^6$) of coho salmon caught in year x by the Oregon commercial troll fishery. Catch data extend from 1942 to 1962. $\text{Catch} (\times 10^{-3}) = -181.0699 + 0.1510 (\text{flow}) (\times 10^{-6})$.
- 5 Total March through May flows ($\times 10^9 \text{ m}^3/\text{sec}$) for five coastal rivers combined versus kilograms ($\times 10^6$) of coho salmon caught one year later by the Oregon commercial troll fishery. Catch data extend from 1942 to 1962. $\text{Catch} (\times 10^{-3}) = 125.7782 + 0.3707 (\text{flow}) (\times 10^{-6})$.

Figure

- 6 Sum of total April through June upwelling indices at 42°N, 125°W, and 45°N, 125°W ($\times 10^6$ kg/sec/100m of coastline) off of Oregon versus kilograms ($\times 10^6$) of coho salmon caught one year later by the Oregon commercial troll fishery. Catch data extend from 1947 to 1962. $\text{Catch} (\times 10^{-3}) = 450.2993 + .00197 (\text{upwelling})$.
- 7 Predicted and observed catch of coho salmon in kilograms by the Oregon commercial troll fishery from 1947 to 1962.

Fig 1

$r = 0.68$

$p < .01$

CATCH

1.5

1.0

0.5

11

13

15

FLOW

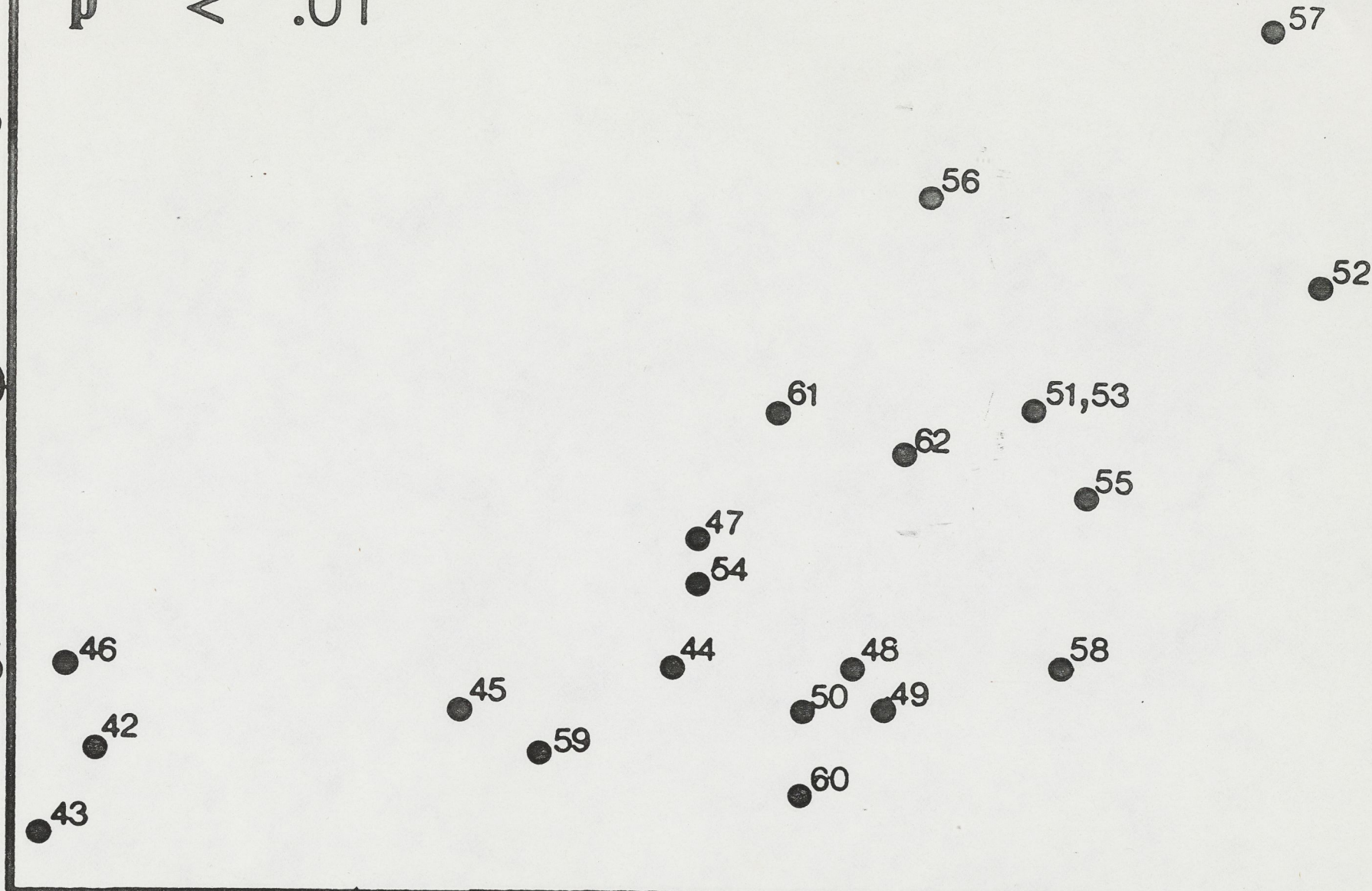
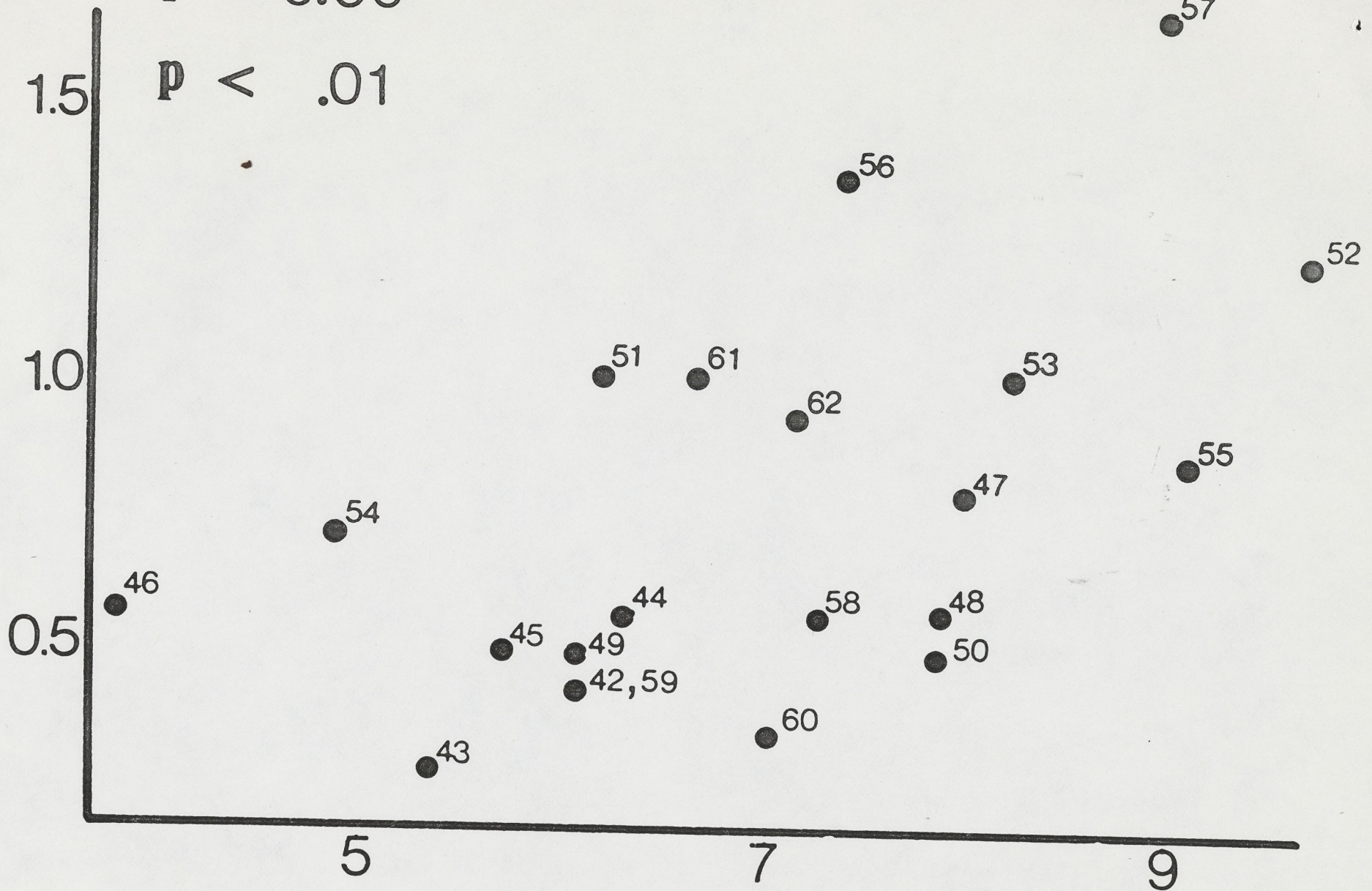


Fig 2

$r = 0.56$

$p < .01$

CATCH



FLOW

Fig 3

$r = 0.28$

$p > .05$

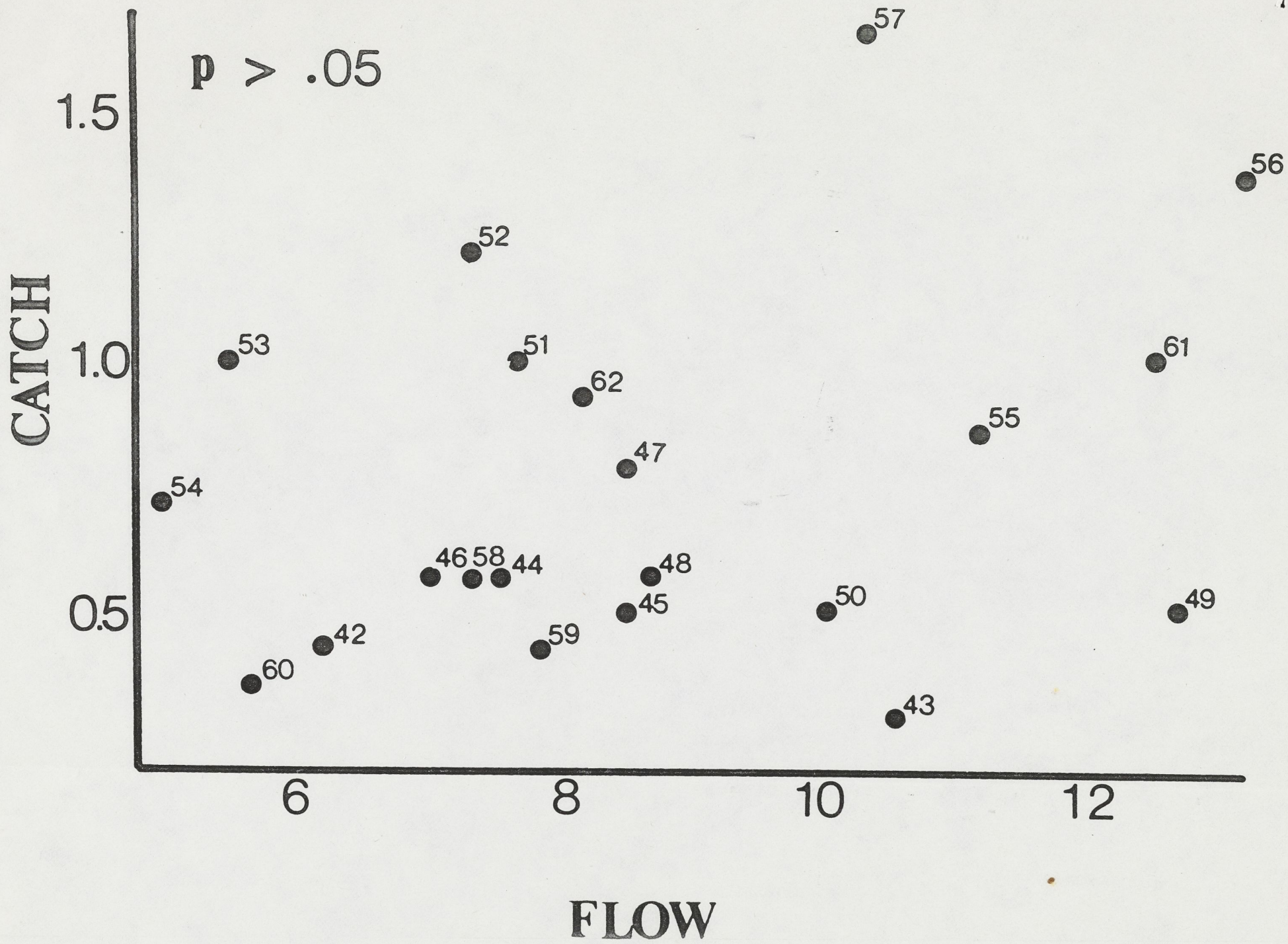


Fig 4

$r = 0.59$

$p < .01$

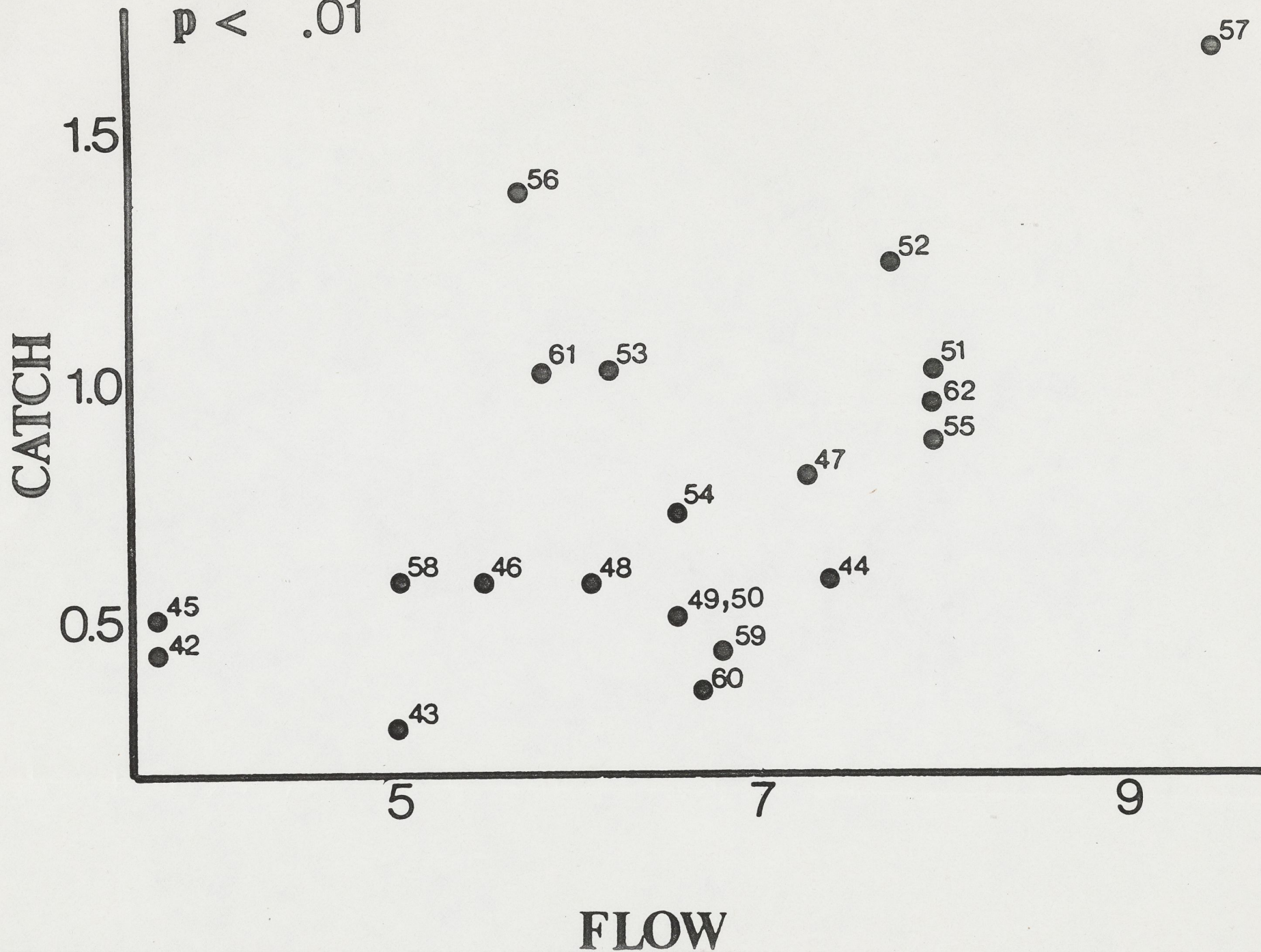


Fig 5

$r = 0.53$

$p < .05$

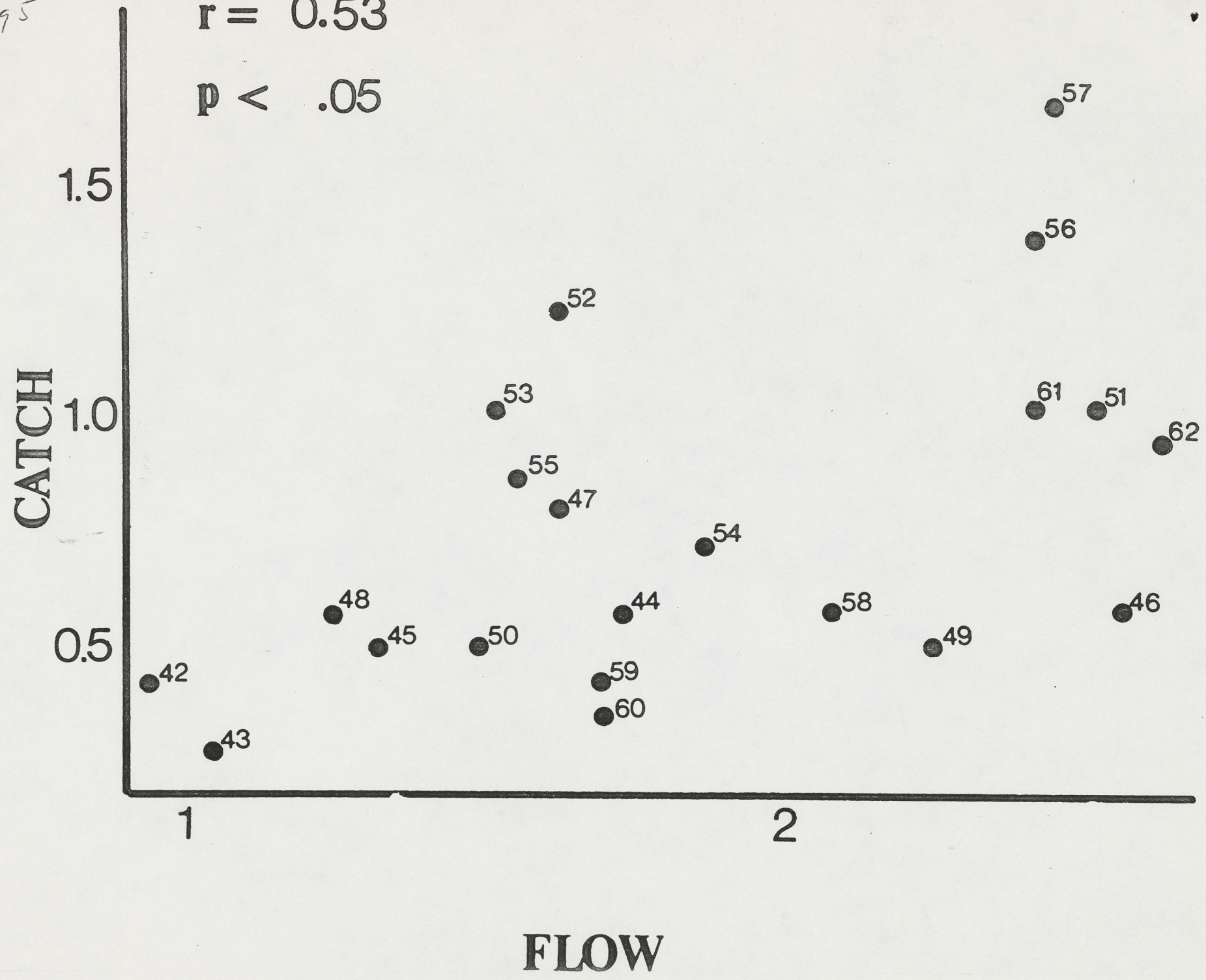
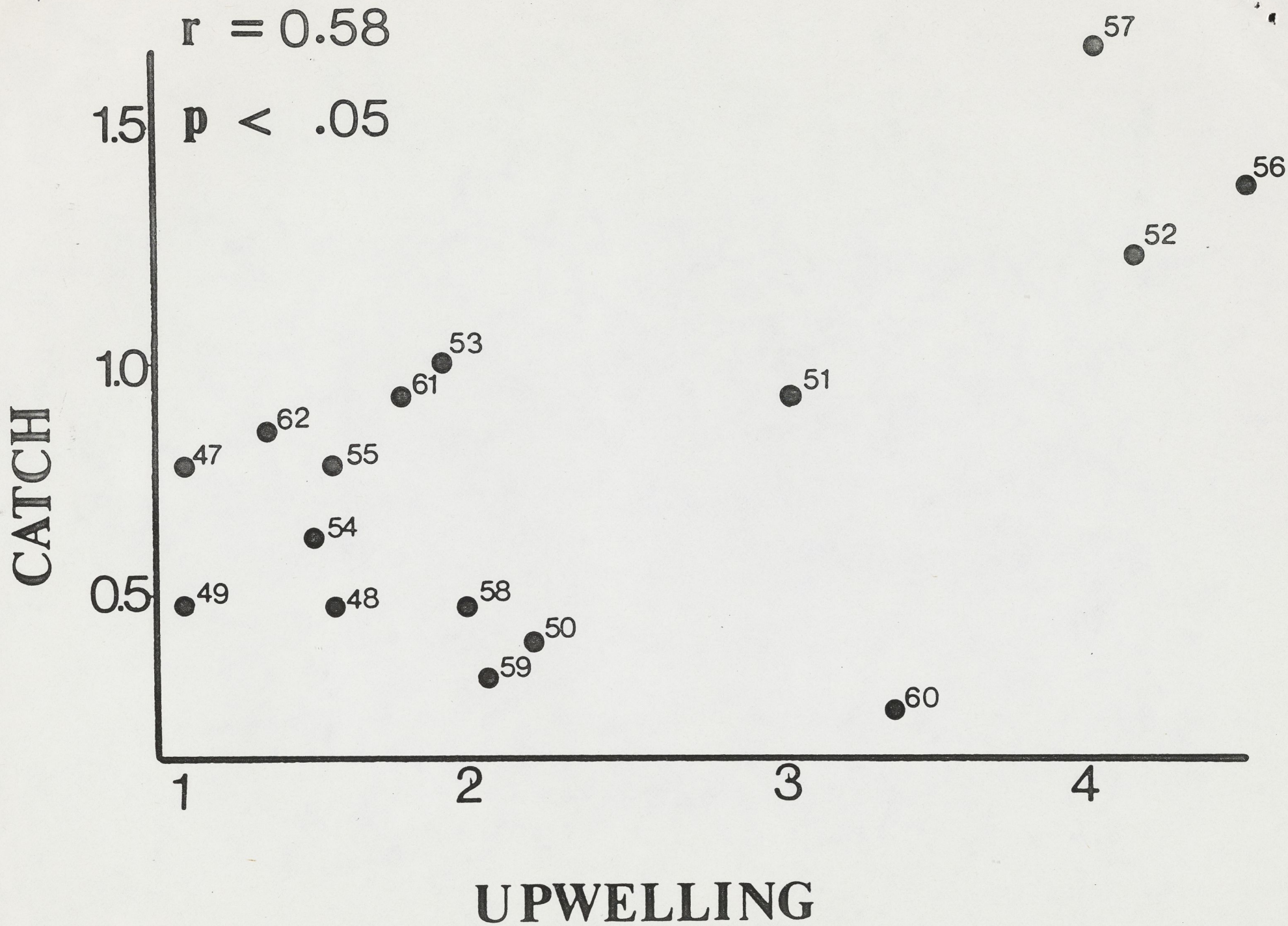


Fig 6



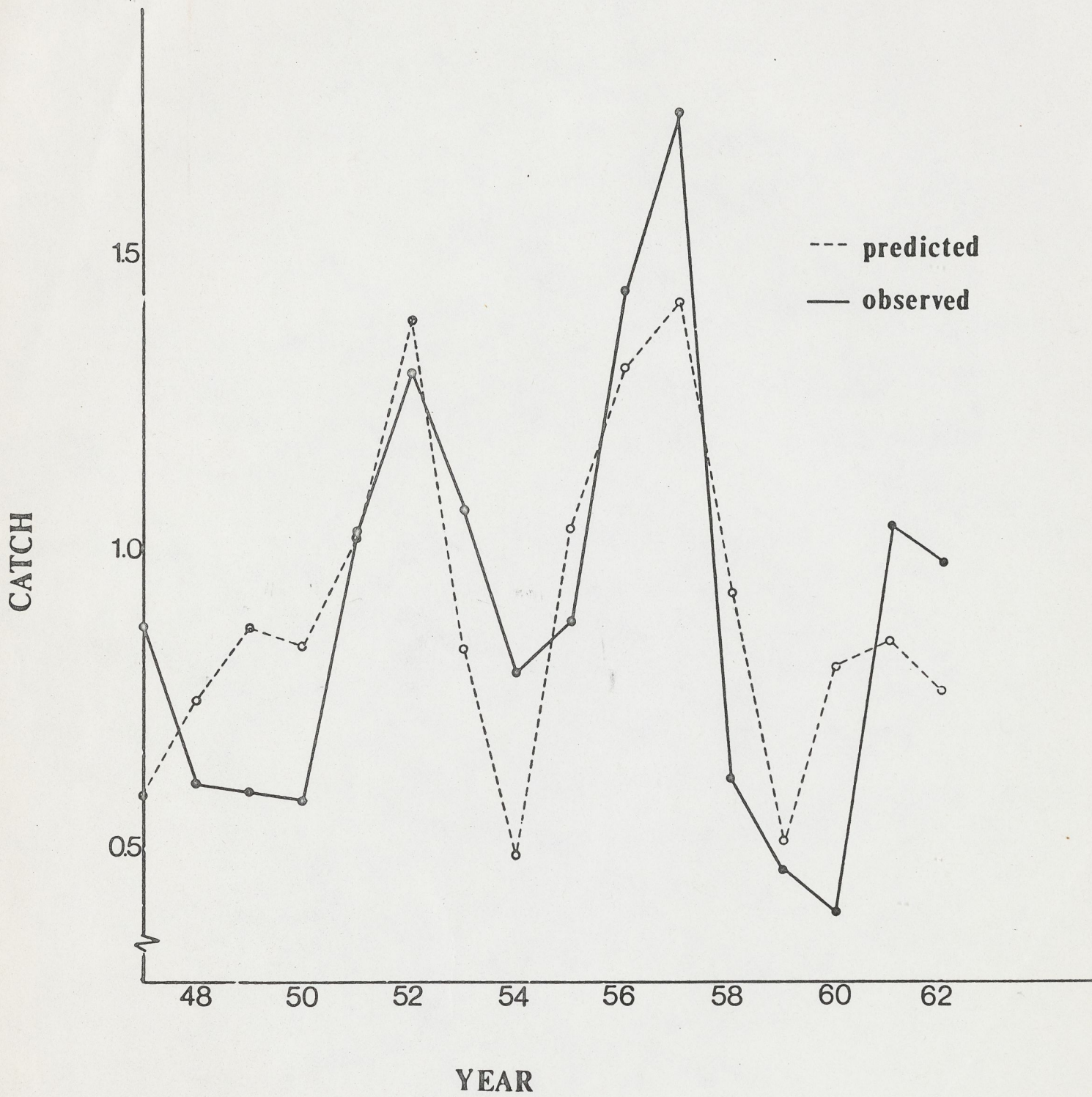


Fig 7

Stunting in brook trout (Salvelinus fontinalis)
populations: causes and remedies.

Dennis L. Scarnecchia
Colorado Cooperative Fishery Research Unit
Colorado State University
Fort Collins, Colorado 80523
April 30, 1979

I. Introduction

The brook trout (Salvelinus fontinalis) is native to the cold water lakes and streams of eastern North America, but its popularity with eastern anglers has led to its introduction into many higher elevation lakes and streams in the Rocky Mountain region (Baxter and Simon, 1970; Everhart and Seaman, 1971; Beckman, 1974). While brook trout are relatively easy to catch and highly edible (Everhart and Seaman, 1971), many fishermen complain of the small size attained by adult fish, especially fish in small streams (Simon, 1946). Many populations of brook trout in Colorado and elsewhere are described as "stunted", i.e., having an overabundance of small, sexually mature fish and few of the larger fish more desirable to anglers. The larger size apparently attained by native cutthroat trout (Salmo clarki) in similar waters is mentioned by biologists and anglers when arguing for reintroduction of native trout into western waters (Allen, 1956). Removal of brook trout from and reintroduction of native trout into many western streams would be expensive, if not impossible, so an alternative, and the objective of this paper, is to consider causes and solutions for stunting of brook trout.

II. The Problem

In my opinion, an attempt to isolate one factor responsible for stunting will fail, since many genetic and environmental factors contribute to the stunting. Stunting can result from the evolved genetic characteristics of individuals, from limitations imposed by environment, or usually a combination of genetic and environmental influences.

The life history of a brook trout population is a product of natural selection acting upon the population during the past. Characteristics such as capacity for individual growth, age of sexual maturity, approximate life span,

incidence of repeat spawning, inter- and intra-specific behavioral traits, have all evolved gradually so that brook trout successfully adapted to eastern streams. These life history characteristics are modified by the particular environment inhabited by the individual fish, so that a fish's capacities (genetic) are not always realized. Thus a fish may be genetically able to grow rapidly or mature sexually early in life under ideal conditions, but these ideal conditions may not exist in the fish's environment. Evolved genetic capacities may be either beneficial or detrimental to brook trout when introduced by men into new waters, depending on the suitability of these water for the trout.

Brook trout appear pre-adapted to many high elevation streams in Colorado, often appearing to out-compete native cutthroat trout for habitat (Binns, 1977). What characteristics make them so efficient at exploiting high mountain lakes and streams?

III. Contributing Causes of Stunting

1. Spawning habits

First of all, brook trout have evolved ability to spawn in diverse standing and running waters (Scott and Crossman, 1973; Webster, 1975). Their requirements for suitable temperatures (Bridges and Mullan, 1958; Vincent and Miller, 1969), suitable flows of water, adequate gravel for spawning (Reiser and Wesche, 1977), and upwelling of groundwater (Webster and Eiriksdottir, 1976) are met in many streams and lakes in Colorado. Hence, abundance of brook trout in many streams is seldom limited by insufficient sites for spawning.

Time of spawning is another evolved trait proving beneficial to brook trout populations. Brook trout spawn in late September to December (Scott

and Crossman, 1973) when flows are stable and low in the Rocky Mountain region. Fry are incubated and hatched prior to high spring runoff from streams, so assuming enough habitat for spawning, survival of fry to emergence in Colorado streams is probably high, as it is in eastern streams (Latta, 1969).

Autumnal spawning of brook trout also gives emerging fry a size advantage over the native cutthroat trout, which spawns during spring. Since the native fish spawn and eggs incubate during higher and more variable flows, native fish might suffer more yearly variation in recruitment of individuals than would brook trout.

2. Age of sexual maturity

A key factor in the proliferation of brook trout in streams is their early age of sexual maturity (Nehring, 1979). In eastern populations, males mature at age 0+ (end of the first summer) while most females mature one year later (I+) (Hunt, 1966, 1974). Although maturation may be delayed a year in some high elevation streams with short growing seasons (Baxter and Simon, 1970), brook trout generally mature one year earlier than native cutthroat trout in comparable streams (Kiefling, 1978; Nehring, 1979). This early maturity results in a high reproductive potential by brook trout too small to be desirable to fishermen, while most or all sexually mature cutthroat trout may be of harvestable size. Hunt (1966) found that in a section of Lawrence Creek, Wisconsin in September 1963 800 age I fish, 200 age II fish, 8 age III and 0 age IV fish were present, and that fishing in the entire Creek acted on mostly age II, III and IV, with higher percentage of age III and IV being caught than of age II. The young spawners provide recruits to the stream even during high fishing pressure on older age classes. This effect

is shown in figure I, which is a reproduction curve (or stock-recruitment relationship) of Ricker (1954). The figure shows the relationship between the number of eggs of parents and number of eggs produced by their progeny. The shape of the curve shows that particular case where to the right of point A, there are enough eggs produced by one year class to produce all of the recruits that a stream could support. Harvest will move the number of eggs produced by the parents to the left. Native cutthroat trout may move left rather quickly towards point A, since most females harvested would be mature. It would be extremely difficult to move brook trout toward point A when many small, mature females would not be harvested. Thus few fish managers have had to worry about eliminating brook trout by fishing. Several states have even encouraged excessive catch of brook trout to lower population densities (Nehring, 1979).

Early age of reproduction and short life spans in brook trout may have evolved in response to their inhabitation of small, unstable streams. In small streams with poor habitat for growth and overwintering of larger fish, it would be advantageous for individuals to spawn at an early age and small size if chances for survival as it grew and overwintered were low (Schaffer and Elson, 1975). An individual should mature at age x if

$$S_x F_x > S_{(x+1)} F_{(x+1)} \quad (\text{Equation 1.}) \quad (\text{Jonsson, 1977})$$

where S and F are age-specific survival and fecundity, respectively. This relationship assumes fitness of individual eggs is constant for all fecundities. In small streams, S_x may be much higher than $S_{(x+1)}$ because of rapidly decreasing amount of habitat for fish as they grow. Larger and older fish may find few places to overwinter and may have difficulty finding cover to escape

from predators. So while fecundity increases with age, it would not counter-balance the decreased rate of survival. Figure II illustrates the maximum combination of survival on fecundity, i.e., when a female fish will optimally mature.

Females generally spawn one year later than males (Hunt, 1966; McFadden, 1961) because larger females may produce larger eggs having higher potential for survival (Jonsson, 1977). There is no evidence that eggs fertilized by larger males survive better than those fertilized by small males. Milt weighs about 7 times less than eggs of a female of comparable size (Jonsson, 1977). Also, since many small male salmonids spawn by darting among a mating pair at the moment of fertilization (Scott and Crossman, 1973), large size may be less of an advantage for males than for females. The female may also require an extra year to accumulate enough energy for successful reproduction (Schaffer and Elson, 1975, Scott and Crossman, 1973).

I conclude that in small streams in temperate regions providing a suitable environment for growth of small fish yet a limited or poor habitat for growth and survival of larger fish, selection would favor evolution of an early maturing fish. Small char (Salvelinus alpinus) maturing late in arctic regions do so because of short growing seasons, so that fish require a year for accumulation of needed energy for spawning. Salmonids in the higher latitudes may then spawn later in life and in alternate years (Schaffer and Elson, 1975).

While early age at maturity would be favored in many small mountain streams where growth and survival of larger fish would be poor, studies on large brook trout from four Canadian lakes (Flick, 1977) indicate that these fish grow rapidly to weights up to 5 kilograms, mature later in life

(at ages II or III) (Webster, 1968), and may live up to 9 years or more. In these lakes, brook trout may spawn in adjoining rivers or in the lakes themselves and most probably rear one or more years in the rivers. Flick (1977) found very few small brook trout in the lakes he studied, either because they were eaten by predators or because they were rearing in streams. Since walleye (Stizostedion vitreum) and northern pike (Esox lucius) were the dominant predators in the lakes (except for walleye being absent from one lake), predation on brook trout fry and fingerlings may have necessitated fry rearing in the rivers until their size precluded predation. In these lakes, brook trout are not a common species, whereas in high-elevation streams in Colorado they may be the only species present.

Based on his studies of food habits, Flick (1977) was unable to identify the food source that produces these large brook trout. So why are these lacustrine brook trout so different from those of Colorado's streams?

Once the brook trout were large enough to enter the lakes without suffering heavy predation, there would be an abundant and predictable food supply of invertebrates since the density of intra-specific competitors would be low. Growth and survival of older age classes would be high. From Equation 1, page 4, it would be beneficial to mature at an older age, as they do, since their fecundity would be much higher each year, yet potential for survival would not decrease much each year.

3. Shortage of habitat for large fish in small streams

While Flick (1977) suggests that some special food supply produces these large trout, perhaps space, not food, is the dominant factor affecting growth and survival in most brook trout populations. Chapman (1966) noted that

regardless of food supply, salmonids have some minimum spatial requirements. Mason (1974) was able to increase summer standing crop of juvenile salmonids six fold by supplemental feeding, yet mortality during the winter eliminated the extra fish of the previous summer; apparently from lack of enough suitable habitat for overwintering. As salmonids grow, their environmental needs become more complex, and spatial requirements increase (Chapman, 1962; Allen, 1969; Symons and Heland, 1978). Hence downstream movement of large fish is often substantial, as they seek suitable habitat (Chapman, 1966). During the summer season when intra-specific competition for space and food may occur in stream-dwelling salmonid populations (Chapman, 1962, 1966), brook trout may suppress their growth in response to limited environments. This argument is supported by Greene's (1955) study of stunted brook trout in Wyoming. When moved to a larger body of water, the stunted brook trout grew rapidly. Many lakes in Wyoming (Simon, 1946) support very large brook trout whereas populations in neighboring small streams may be stunted. In small streams, selection would favor fish having and exercising the ability to limit and adjust their growth rates while remaining healthy. Such repression may be from ammonia or other chemicals released into the water (Bennett, 1970) or a stress response resulting from overcrowding and consequent diversion of food from assimilation, or from other factors. Many mechanisms may be controlled by the physiological responses of individual fish. Stunting may then be viewed as a selectively advantageous response by the individual. Just as a goldfish would not outgrow its aquarium, a brook trout would not outgrow its stream habitat. Fish such as those of the large Canadian lakes (Flick, 1977) would be selectively favored if they grew rapidly and would not generally repress their growth.

4. Lack of predation

Predation (or lack of it) of brook trout by other species of fish may also influence stunting of populations. As mentioned, walleye and northern pike are potential predators of young brook trout in large Canadian lakes (Flick, 1977). Alexander (1977) found brown trout (Salmo trutta) eating 51% and 39% of the ages I and 0 brook trout, respectively, in Michigan's Au Sable River. If substantial reduction of biomass of age 0 and I fish would significantly lessen densities of fish, stunting due to overcrowding may be lessened, assuming there is enough suitable habitat for larger fish. Biomass may then be distributed into fewer but larger fish. In most high mountain streams, however, no such piscine predator occurs. Although kingfishers (Family Alcedinidae) and merganser (Family Anatidae, subfamily, merginae) may significantly reduce survival of salmonids through predation (Elson, 1962), the high population densities of brook trout in western streams attest to these predators' inability to eliminate stunting. As Alexander (1977) suggests, avian and mammalian predators may primarily eat larger fish and fewer smaller fish.

In the Au Sable River, it is debatable whether less stunting would occur from efficient predation by brown trout or from the rather large (width of stream is 30 m) riverine habitat providing space for growth of large fish. A combination of adequate food and adequate rearing space for the larger mature fish, as well as substantial predation on smaller fish, may effectively eliminate stunting problems.

5. Territory sizes--are they smaller for brook trout than other trout?

Following emergence of fry from their eggs, young trout in streams become territorial (Newman, 1956) with dominant fish assuming their preferred

areas in the stream. Establishment and defense of territories are documented for Atlantic salmon, brown trout (Kalleberg, 1958), coho salmon (Chapman, 1962; Hartman, 1965; Mason and Chapman, 1965) and other salmonids. It is logical to ask if the size of territory defended by brook trout is smaller than that of cutthroat trout for a given food supply and a given size of fish. If so, the biomass of brook trout may be distributed into more and smaller individuals. This is an area for future research.

IV. Possible Remedies for Stunting

One possible remedy for stunting is to stock in streams those brook trout maturing at ages II and III and not those maturing very early in life. Fishing mortality might then lessen total fecundity and lead to lower recruitment, and possibly better growth. I dislike this remedy if used by itself on small streams because lack of available space for growth and overwinter survival may still limit growth and survival of large fish.

For many small streams, the preferable remedy is stream improvement (see Lagler, 1956; Hunt, 1969). Wisconsin biologists altered sections of Lawrence Creek to greatly increase pool area and overhanging stream bank cover. Production of age II and III fish was increased by 133% and 700% respectively, while production of age 0 fish did not change and that of age I increased 17%. So survival of older fish was vastly improved by their practices. Hunt (1966) suggested that increased rates of overwinter survival led to increased production of larger fish.

Stream improvement practices have been successful in trout management. Yet beavers (Castor canadensis) construct dams in many brook trout streams in Colorado and elsewhere with questionable or variable benefit to brook trout population (Rutherford, 1964). Documented changes in streams following

construction of dams include retardation of flow and consequent rise in water temperature, destruction of shade-producing trees and shrubs by drowning, accumulation of excessive silt and organic debris in front of the dams, increased incidence of diseases and parasites of fish (Knudsen, 1962), and radical changes of benthic invertebrate fauna (Sprules, 1940). Knudsen (1962) suggests that in many streams trout habitat is improved for a few years following construction of dams, but that excessive siltation, organic deposition, and other factors lead to deterioration of habitat. Furthermore, beaver ponds may freeze in winter because of severely limited inflowing water and contribute little to overwintering habitat. Siltation of spawning beds is also a by-product of beaver dams. Stream improvements such as log and stone current deflectors could provide deeper pools required by larger fish yet not completely restrict flows nor lead to the problems associated with beaver dams. Stream improvement practices should be implemented to provide better and more feeding and overwintering habitat for larger fish, without causing excessive siltation and organic deposition in these areas.

Combined with stream improvement practices, management might impose a catch limit on large mature fish but no limits on the removal of smaller fishes recently mature or still immature. The resulting heavier harvest of smaller fish would reduce population densities and distribute total stream biomass among fewer but larger fish. Hopefully, fishermen would still harvest these small fish. These regulations might work well on small streams in combination with stream improvement practices, but probably would not work by themselves (Baxter and Simon, 1970).

Stocking of predaceous fish in small streams is not feasible because of lack of adequate species that could coexist with brook trout. Results of such stocking in lakes are unpredictable so that stocking is not advisable.

V. Summary

Contributing causes of stunting of brook trout are:

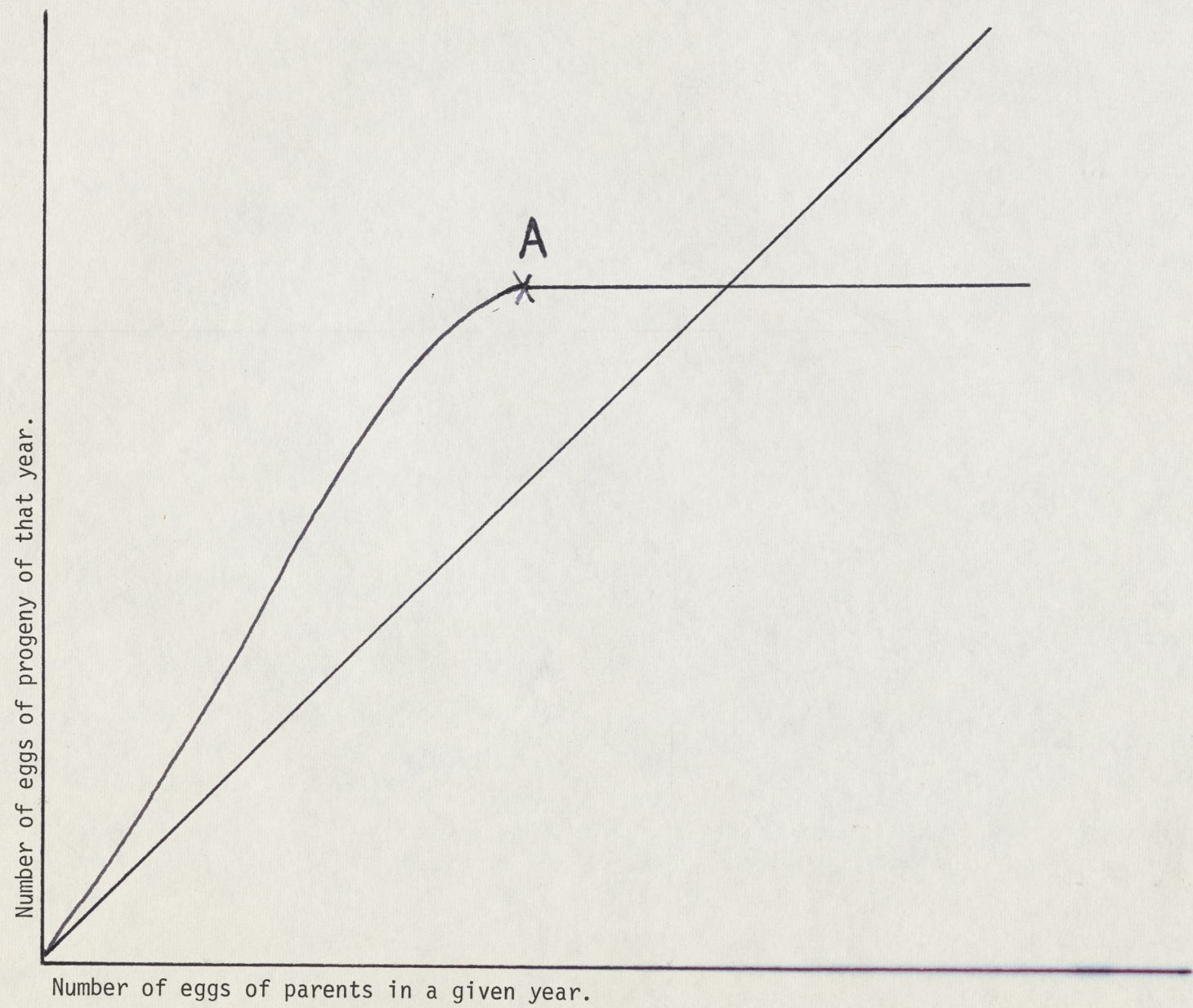
- (1) highly successful spawning in suitable lake and river environments;
- (2) timing of spawning yielding high survival of eggs;
- (3) early age of sexual maturity in many stocks;
- (4) little fishing pressure or natural predation of younger fish in many streams;
- (5) limited space for growth and overwinter survival of larger fish in small streams.

The preferable remedy is stream improvement combined with regulations encouraging harvest of smaller fish and restricting harvest of largest fish.

- Alexander, G. R. 1977. Consumption of small trout by large predatory brown trout in the North Branch of the Au Sable River, Michigan. Michigan Dept. Nat. Res. Fish. Res. Rep. 1855. 26 pp.
- Allen, G. H. 1956. Age and growth of brook trout in a Wyoming beaver pond. Copeia. No. 1:1-9.
- Allen, K. R. 1969. Limitations on production of salmonid populations in streams. In T. G. Northcote, editor, Symposium on Trout and Salmon in Streams. p. 3-18. H.R. Macmillan lectures in fisheries. Univ. of British Columbia. Vancouver.
- Baxter, G. T., and J. R. Simon. 1970. Wyoming Fishes. Revised edition. Wyoming Game and Fish Dept. Bull. 4, Cheyenne. 168 pp.
- Beckman, W. C. 1974. Guide to the fishes of Colorado. Univ. of Colorado Museum, Boulder. 110 pp.
- Bennett, G. W. 1970. Management of lakes and ponds. Van Nostrand Reinhold, New York. 375 pp.
- Binns, N. A. 1977. Present status of indigenous populations of cutthroat trout, Salmo clarki, in southwest Wyoming. Wyoming Game and Fish Dept. Fish. Tech. Rep. 2. 58 pp.
- Bridges, C. H., and J. W. Mullan. 1958. A compendium of the life history and ecology of the eastern brook trout Salvelinus fontinalis (Mitchill). Mass. Div. Fish. and Game Fish. Bull. 23. 30 pp.
- Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19:1047-1080.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. The Amer. Nat. 100:345-357.
- Elson, P. F. 1962. Predator-prey relationships between fish-eating birds and Atlantic salmon. Bull. Fish. Res. Board Can. 133:87 pp.
- Everhart, W. H., and W. R. Seaman. 1971. Fishes of Colorado. Colorado Game, Fish and Parks Division, Denver. 75 pp.
- Flick, W. A. 1977. Some observations, age, growth, food habits and vulnerability of large brook trout (Salvelinus fontinalis) from four Canadian lakes. Nat. Can. 104:353-359.
- Greene, A. F. C. 1955. Will stunted brook trout grow? Prog. Fish. Cult. 17:91.

- Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 22:1035-1081.
- Hunt, R. L. 1966. Production and angler harvest of wild brook trout in Lawrence Creek, Wisconsin. Wis. Conserv. Dept. Tech. Bull. 35. 52 pp.
- Hunt, R. L. 1969. Effects of habitat alteration on production, standing crops, and yield of brook trout in Lawrence Creek, Wisconsin. In T. G. Northcote, editor. Symposium on salmon and trout in streams. p. 281-312. H. R. MacMillan lectures in fisheries. Univ. British Columbia, Vancouver.
- Hunt, R. L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wis. Dept. Nat. Res. Tech. Bull. 82. 29 pp.
- Jonsson, B. 1977. Demographic strategy in a brown trout population in western Norway. Zool. Scr. 6:255-263.
- 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. Freshw. Res. Drottning. 39:55-98.
- Kiefling, J. W. 1978. Studies on the ecology of the Snake River cutthroat trout. Wyoming Game and Fish Dept. Fish. Tech. Rept. 3. 198 pp.
- Knudsen, G. J. 1962. Relationship of beaver to forests, trout and wildlife in Wisconsin. Wisconsin Conserv. Dept. Tech. Bull. 25. 52 pp.
- Lagler, K. F. 1956. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 421 pp.
- Latta, W. C. 1969. Some factors affecting young-of-the-year brook trout, Salvelinus fontinalis (Mitchill) in streams. In T. G. Northcote, editor. Symposium on salmon and trout in streams. p. 229-240. H.R. MacMillan lectures in fisheries. Univ. British Columbia, Vancouver.
- Mason, J. C. 1974. A further appraisal of the response to supplemental feeding of juvenile coho (O. kisutch) in an experimental stream. Can. Fish. and Mar. Serv. Tech. Rep. 470. 26 pp.
- Mason, J. C., and D. W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Board Can. 22:173-190.
- McFadden, J. T. 1961. A population study of the brook trout, Salvelinus fontinalis. Wildl. Monogr. 7. 73 pp.
- Nehring, R. B. 1979. Bonus brook: bane, boon or bonanza. Colorado Outdoors. 28:16-20.

- Newman, M. A. 1956. Social behavior and inter-specific competition in two trout species. *Physiol. Zool.* 29:64-81.
- Reiser, D. W., and T. A. Wesche. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. *Univ. Wyo. Water Res. Res. Inst. Ser. No. 64.* 100 pp.
- Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 9:559-623.
- Rutherford, W. H. 1964. The beaver in Colorado. Its biology, ecology, management, and economics. Colorado Game, Fish and Park Dept. Tech. Pub. 17. 49 pp.
- Schaffer, W. M., and P. F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology* 56:577-590.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. *Fish. Res. Bd. Can. Bull.* 184. 966 pp.
- Simon, J. R. 1946. Wyoming fishes. Wyoming Game and Fish Dept. Bull. 4, Cheyenne. 129 pp.
- Sprules, W. M. 1940. The effect of a beaver dam on the insect fauna of a trout stream. *Trans. Am. Fish. Soc.* 70:236-248.
- Symons, P. E. K., and M. Heland. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (Salmo salar). *J. Fish. Res. Board Can.* 35:175-183.
- Vincent, R. E., and W. H. Miller. 1969. Altitudinal distribution of brown trout and other fishes in a headwater tributary of the South Platte River, Colorado. *Ecology.* 50:464-466.
- Webster, D. ed. 1975. Proceedings of brook trout seminar. Whiting Hotel, Stephen's Point, Wisconsin, Sept. 22-24, 1975. 16 pp.
- Webster, D. W. 1968. Bradon Park fish management report. pp.
- Webster, D. W., and G. Eiriksdottir. 1976. Upwelling water as a factor influencing choice of spawning sites by brook trout (Salvelinus fontinalis). *Trans. Am. Fish. Soc.* 105:416-421.



Number of eggs of parents in a given year.

Figure 1. Stock recruitment relationship (from Ricker, 1954).

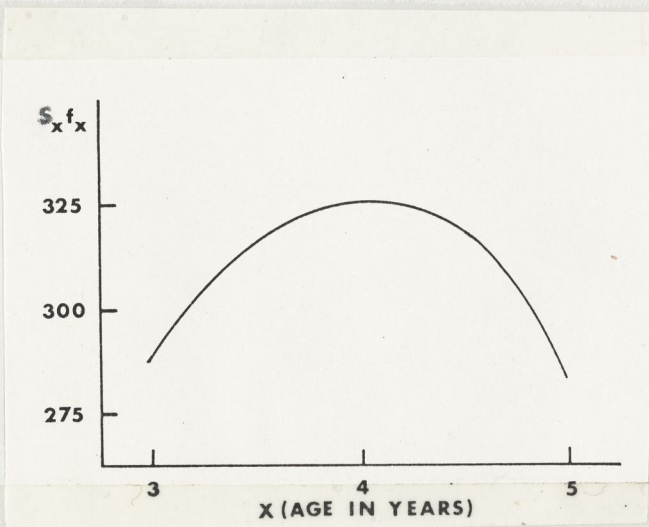


Figure 2. Survival-fecundity curve showing age IV as optimal age of maturity.

(From Jansson, 1977)

The errors likely in ageing roach *Rutilus rutilus* (L.), with special reference to stunted populations

✓
Drupe

by R. S. J. LINFIELD

Freshwater Fisheries Unit, Department of Zoology, University of Liverpool, England.*

SUMMARY

1. Features to be found on the scales of roach are briefly described with reference to the work of previous authors.
2. It is demonstrated that roach in the 1968 year class from Grey Mist Mere (South Lancashire, England) formed two checks on both their scales and opercula in their second year of life. The two checks were separated by a pronounced season of winter growth and both were initially accepted as annuli.
3. Methods of error detection are briefly reviewed and applied to the scales of fish in the 1968 year class from Grey Mist Mere. None of the commonly used methods are found to be totally satisfactory.
4. Other sources of error are reviewed. It is concluded that errors are particularly likely to occur with stunted populations but that they will have less effect on the final results of growth studies than similar errors made in ageing 'normal' or fast growing populations.
5. The difficulty in carrying out adequate proofs of validity in populations which have irregular growth patterns is considered a major problem in ageing roach. The value of long-term studies is stressed.

1. INTRODUCTION

The scales of roach *Rutilus rutilus* (L.) have been described by Masterman (1923), Segerstrale (1932), Hartley (1947) and Jones (1953). A detailed histochemical study on the features of roach scales used in ageing has been carried out by Wallin (1957). The work of these authors, and others, has led to the general acceptance of scale reading as a useful technique for ageing roach. The validity of the method has been demonstrated many times but it will be shown in this paper that errors can occur in several ways and with sufficient frequency to significantly affect the results of population studies.

2. BASIC METHODS USED FOR AGEING ROACH

Most workers have found that the growth of roach slows or stops completely during the winter months and that the annual checks ('annuli') are formed at the scale edge of most fish when growth resumes in the summer. Each annulus appears as a number of closely spaced rings (or ridges) in the anterior field and as a single robust ring of thickened material in the posterior field. From about the third year of life re-absorption of material from the scale edge

often takes place during the growth stoppage and results in an 'erosion mark' in the position of the annulus. The erosion tends to be most pronounced at the anterolateral corners of the scales, accentuating the phenomenon known as 'cutting-over' of the rings, and is often referred to as a spawning mark.

The opercular bones of the roach also show the annual patterns of growth quite clearly. Banks (1970) preferred the use of opercula to scales in ageing roach from a fast-growing population and they have also been found useful when working with stunted fish (Linfield, 1971). In years when stunting is particularly severe, erosion often obliterates a full season's growth on the scales but has relatively little effect on the opercula. The method of ageing roach from their opercula is basically the same as that described for perch (*Perca fluviatilis* L.) by Le Cren (1947), and the annuli are taken as the leading edge of the opaque summer bands. Throughout this paper the emphasis will be on the use of scales for ageing roach but the remarks made will be equally applicable to the opercular.

It is generally recognised that all species of fish are liable to form 'false checks' on their scales and other bony structures at various times of the year. A true annulus can be followed right around the scale and is a constant feature on all of the scales examined from any one fish. It has therefore become a fairly routine practice in ageing to accept as annuli only those checks which fit this description. When both scales and opercula are used for ageing it is also a helpful procedure to cross-match the checks on the two types of bony structure and to accept as annuli only those checks which can be clearly identified by both methods. The first check (and possibly the second) is excepted from this rule because it is usually obliterated on the opercula of older fish by basal thickening of the bone.

3. CHECK FORMATION ON THE SCALES OF THE 1968 YEAR CLASS OF ROACH FROM GREY MIST MERE

In Grey Mist Mere, which is an 8½ acre lake in South Lancashire, roach in the 1968 year class are the progeny of a population recovering from a period of severe stunting (Linfield, 1973). A preliminary study on the population was carried out in May 1969 and followed by more detailed work commencing in November of that year.

From November 1969, samples of fish were taken from the lake near the middle of each month over a two year period. All the roach were aged using the combination of scales and opercula with the methods described above. In addition, the number of scale rings outside what was initially accepted as the last annulus (the 'plus growth') was recorded for each fish, using the average value from three scales. The 1968 and 1969 year classes were dominant in the

* Present address: c/o Glamorgan River Authority, Tremains House, Coychurch Road, Bridgend, Glamorgan.

samples, at different times, and each was treated separately from the other age groups. The data were combined into bimonthly samples and the number of scale rings outside the last annulus plotted as a series of frequency histograms. In Fig. 1 it can be seen that the frequency distribution for the 1968 year class in November/December 1969 was markedly bimodal. This resulted from the fact that a large proportion of fish in the year class formed a second check on their scales in the Autumn of 1969 which had been accepted as an annulus (Plate 1). The fish had been aged as two years old but retained in the 1968 year class on the assumption that they had formed their second annulus early. On a second reading of the scales and opercula it was discovered that a check which had not been accepted as an annulus could also be identified in a corresponding position on the scales of some of the other fish in the year class and that at least some form of irregularity could be found on the scales of most of them.

As the winter progressed the number of fish with an annulus near the scale edge became less. The shape of the frequency distribution changed and the mean number of rings outside the last annulus increased markedly (Fig. 1). In March/April the 'plus growth' on the scales was, on average, nearly 50% greater than in November/December, the mean number of rings outside the last annulus having increased from 16 to 24. This pronounced season of winter scale growth was reflected in a measurable increase in the length of the fish. The mean fork length \pm standard error increased from 79.20 ± 0.73 mm in November/December to 84.42 ± 0.85 mm in March/April. From Fig. 2 it can be seen that most of this growth took place in the latter half of the winter. Similar growth has previously been recorded by Williams (1967) for roach from the River Thames. Data for the 1969 year class of roach was inadequate to demonstrate the pattern of scale growth in the winter of 1969/70. For the combined pre-1968 year classes, some fish had an annulus near the scale edge during the winter but the frequency distribution for the number of rings outside the last annulus was not bimodal and gave a mean value of 11 in both the early winter and the spring.

Fish of all age groups formed an annulus on their scales between May and July in 1970 (Fig. 1). As the pre-1968 year classes had not grown significantly during the 1969/70 winter, those fish which had a check at the scale edge during this period still showed only 1 annual check for the 1969-70 year. The autumn/winter formed check became part of the annulus formed in early summer when growth was resumed. As most of the 1968 fish had formed a check in the Autumn of 1969, followed by a period of fast scale growth, the check formed in May-June 1970 was at least the second formed in the 1969-70 year.

It has been shown that a large proportion of the autumn-formed checks were indistinguishable from true annuli and as a result of this many of the fish from the 1968 year class were initially over-aged after the true second annulus had been formed.

Autumn formed checks on roach scales have also been identified by Karpinska-Walus (1961) who gave the following explanation: 'As the formation of check on roach scale is connected with the increase of the rate of its growth, the annulus is formed every year, at the moment when the new current season growth starts. If, during the same year, the rate of growth is obviously increased again, for some reason, the false

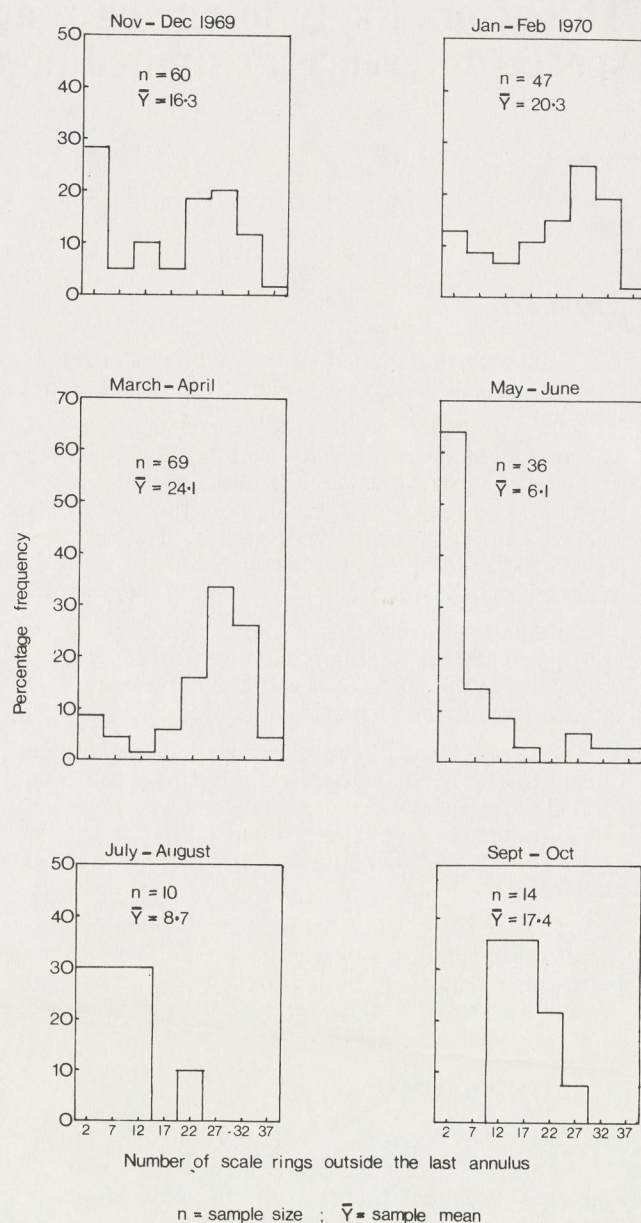
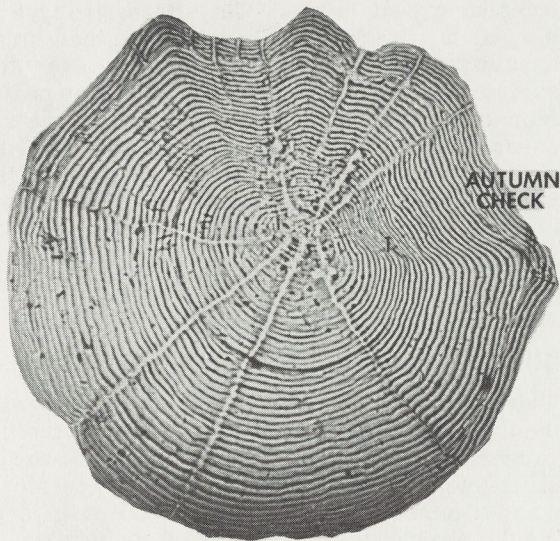


Fig. 1. Scale growth in the 1968 year class of roach from Grey Mist Mere

check appears on the scale.' The data on the 1968 year class from Grey Mist Mere supports this view.

After completion of the second year's growth many fish in the 1968 year class could only be aged correctly because of chance circumstances surrounding the study. First, the project had been started at a time when it was possible to show that the fish had formed an autumn check in 1969 and that the formation of this check was followed by a season of pronounced winter scale growth. Secondly, the 1967 year class (and the 1966 class) was almost totally absent from the fishery and therefore doubts immediately arose about the true age of the large number of fish appearing in this class during 1970. Thirdly, through a combination of many factors the growth of roach in Grey Mist Mere improved dramatically after the winter of 1967/8 and the very few 1967 fish caught during the project could be distinguished from the 1968 fish because the length ranges of the two age groups did not overlap.



(a) 1968 year class, caught 21. 11. 69



(b) 1969 year class, caught 11. 6. 70

Plate 1. Scales of roach from Grey Mist Mere

4. EFFECTIVENESS OF COMMONLY USED METHODS OF ERROR DETECTION

Having described how roach in the 1968 year class from Grey Mist Mere formed an extra check in their second year, it is interesting to consider how such a check might be correctly interpreted if it was formed in a population prior to the commencement of age and growth studies. It has been demonstrated that the standard practice of accepting only those checks which can be followed all around the scales, and which are constant features of all scales examined from any one fish, are not always effective in this respect. The autumn check in the 1968 year class could be satisfactorily matched up with a corresponding check on the opercula. Thus the combined use of more than one type of bony structure for ageing is of limited value in preventing this particular type of error.

The modes of a length frequency distribution (Petersen Method) can often be used to check the ages of at

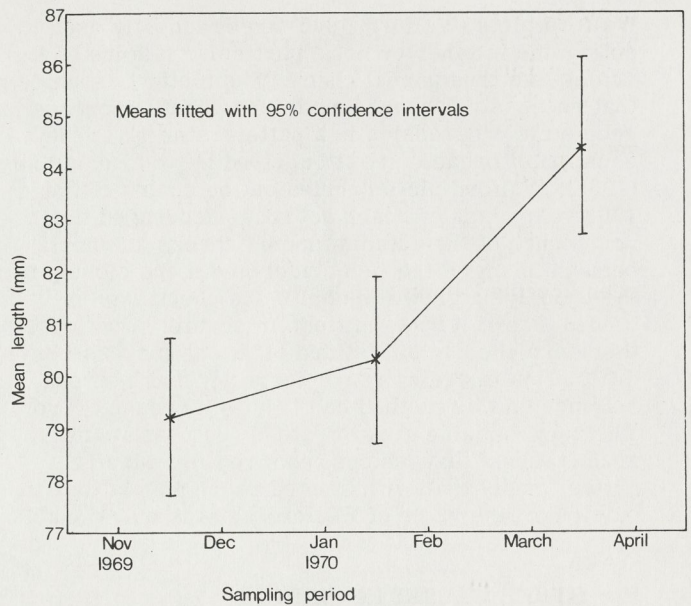


Fig. 2. Winter growth in the 1968 year class of roach from Grey Mist Mere

least the younger fish in a sample and this method is particularly useful for studies on fast growing populations. With stunted populations, however, it is of limited value because the length frequency distributions of all the age groups, except the first, overlap to such an extent that their modes cannot be identified. A sample of 258 roach taken from Grey Mist Mere in May 1969, before the improved growth rate had noticeably affected the population, had a unimodal length frequency distribution (Fig. 3). No one year old fish were included.

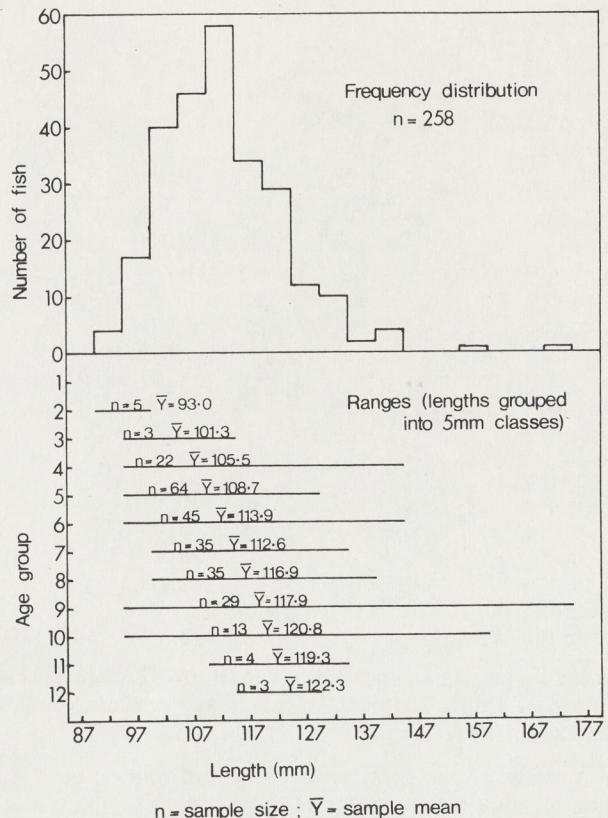


Fig. 3. Length data for roach from Grey Mist Mere in May 1969

Walford plots (Walford, 1946) are frequently used to determine whether or not a particular feature on the scales is a true annual check. The method assumes that successive annual length increments decrease in geometric progression in a pattern similar to the equation of organic growth derived by von Bertalanffy (1938). Walford plots carried out on scales of the 1968 year class of roach actually encouraged the acceptance of the autumn formed checks as annuli because many of the fish conformed more closely to the underlying growth model if the check was included than if it was omitted. In certain situations, therefore, the use of Walford plots can increase the difficulties in ageing roach correctly and a strong reliance on this method can lead to increased error. The very variable growth rate of the roach causes such frequent digressions from von Bertalanffy's growth model that, with stunted roach populations in particular, the value of Walford plots is questionable.

5. OTHER CAUSES OF ERROR

(i) The position of the first annulus

A common difficulty in ageing roach lies in establishing the position of the first annulus. This is very variable between year classes but fairly constant within any one year class.

In a poor summer, when breeding occurs late and the fry do not hatch until late June or early July, the first year's growth may be very poor, with only a few scale rings being formed inside the first annulus (Plate 2). In contrast, in a good year, when breeding occurs early and the growing season extends well into the autumn, the first year's growth may be considerably greater and more than twenty scale rings may be formed inside the first annulus (Plate 1).

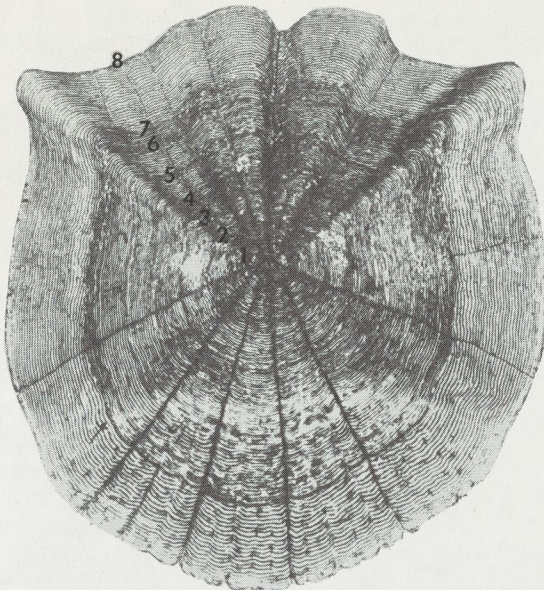


Plate 2. Scale from a roach of the 1962 year class from Grey Mist Mere, caught 10. 6. 70

In a study where first year growth of one or both extreme types is encountered on the scales, two types of error can easily be made. First, an annulus very near to the centre may be dismissed as a false check if it is only encountered in one or two year classes.

This error is particularly likely to occur if the second year growth is poor. The alternative type of error may occur with fish that have formed their first annulus an exceptionally great distance from the scale centre. When compared with scales of fish from other year classes these fish will appear to have been too big for their apparent age when the first visible annulus was formed. The assumption is then likely to be made that the first visible annulus is in fact the second and, if the exceptionally good first year is followed by several poor ones, this assumption may be further encouraged by the use of Walford plots.

(ii) The interpretation of two closely spaced checks

When an apparently poor year's growth is present on the scales of a roach population (Plate 2) the investigator has to make a decision on which of two possibilities to accept. Either, the two checks which appear close together are both annuli and the rings separating the two checks represent a whole year's scale growth, or, one of the two checks is a false check, formed either near the beginning or near the end of a relatively 'normal' year's growth. Unfortunately, when faced with this problem there is usually no way in which a worker can be sure of making a correct decision. Chance circumstances affecting a particular study may enable this to be done but more often than not the investigator is forced into making a decision based largely on intuition.

Practical circumstances usually dictate that a study of a particular fish population involves regular sampling for a relatively short period of time (rarely more than two years). If check formation is observed to be strictly annual during this period, acceptance of the validity of scale reading as a method of ageing will tend to lead to the acceptance as annuli of all scale checks resembling those formed during the sampling period. If it should happen that two pronounced checks are formed close together in the same year during a sampling period, then this observation will tend to encourage the belief that similarly spaced checks from previous years were formed in the same way. As the growth of roach may be highly variable from year to year, it does not follow that the pattern of check formation observed during the sampling period is necessarily identical to that of previous years. As the true pattern of scale growth in these years cannot always be assessed with confidence, the occurrence of closely spaced checks on roach scales presents a problem of interpretation that will inevitably lead to occasional errors in age and growth studies. This problem is illustrated, and has been discussed, in previous work by Cragg-Hine (1965) and Cragg-Hine and Jones (1969). The problem is most acute when working with scales from stunted populations because most of the annuli are laid down very close to one another (see below).

(iii) Additional errors likely in ageing roach from stunted populations

The annual growth increments of fish from severely stunted populations can be so small in some years that the annuli become almost superimposed. In these circumstances severe erosion at the scale edge can result in the partial or even complete obliteration of several season's growth. Similar problems can also occur at the scale edge of exceptionally old fish from more 'normal' populations. Fortunately the opercular bones are not so susceptible to erosion and checks

that might otherwise be missed can usually be identified by cross-matching the features to be found on the opercula with those on the scales (Plate 3).

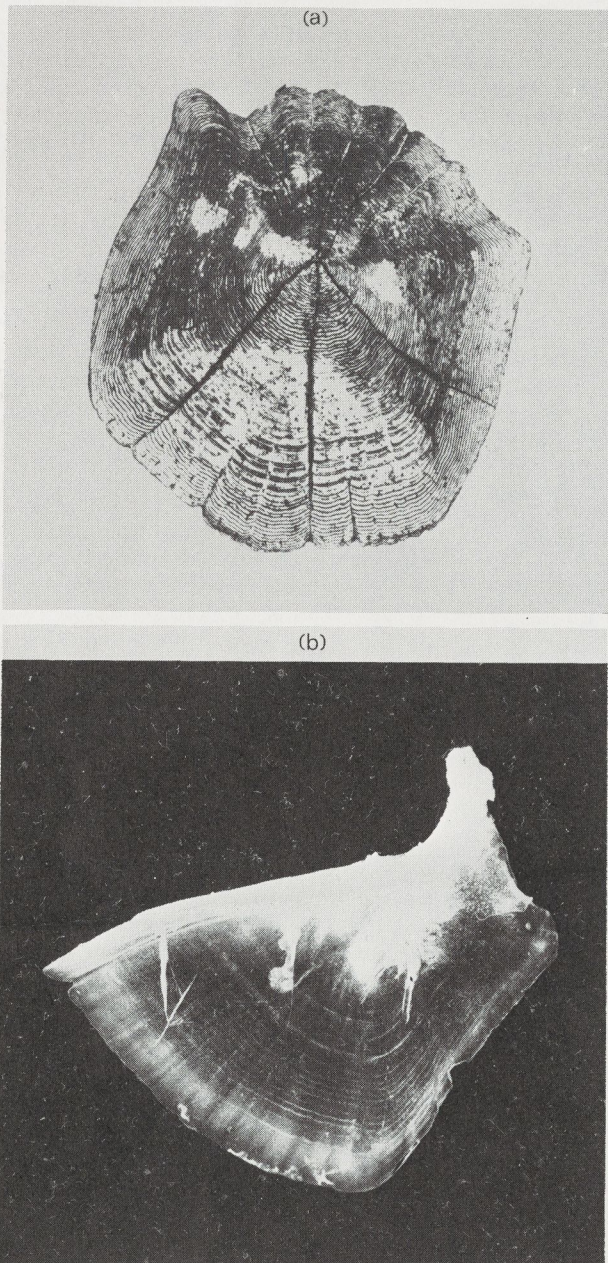


Plate 3. A scale (a) and an operculum (b) from a severely stunted roach (length 156 mm) from Grey Mist Mere. The fish was tentatively aged as 13⁺⁺

False checks are common on the scales of stunted fish and their recognition is made particularly difficult by the fact that all the fish have a check near the scale edge throughout the year as a result of their very small growth increments. Although most false checks can be identified by their inconsistent appearance, it is difficult to be sure that the checks accepted as annuli have in fact been formed on an annual basis. Validity tests involving the progression of a dominant year class, or the sudden decrease in the average length of an age group after an annulus has been formed, cannot often be used with severely stunted populations. Several successive strong year classes are usually present (the overcrowding this produces being a con-

tributory factor to the cause of stunting) and their length frequency distributions may overlap to such an extent that their mean lengths are not significantly different (Fig. 3). Stunted populations therefore cause the most difficulties in ageing but it is interesting to note that errors in ageing such populations have far less effect on the final results of growth studies than similar errors made on 'normal' or fast growing populations. From about the third year of life the mean lengths of adjacent age groups in severely stunted populations differ so little that an error of one or two years in ageing many of the fish would make little difference to the overall results and the final conclusions. In fast growing populations a similar number of errors would have a much greater effect on the data and would therefore result in much greater errors being made when the final conclusions are drawn.

6. CONCLUSION

The variable growth rate of the roach produces irregularities in the annual pattern of scale growth which can lead to errors in ageing. The acceptance of false checks as annuli is considered the most likely error because such checks can be formed in ways which will not be shown up by standard techniques for error detection. Errors can also result from the rejection of annuli as false checks or from their being missed because they have become superimposed or obliterated. The non-formation of scale annuli has not been considered as a cause of error because it is not thought to be a common problem in ageing roach. The first annulus may sometimes be indistinct but is usually recognisable.

Stunted roach are particularly difficult to age but the final results from growth studies on stunted populations are less affected by errors than the results from studies on 'normal' or fast-growing fish. Currently used ageing technique may generally yield fairly accurate results in studies on roach populations but the method so often necessitates the making of decisions based on inadequate proofs of validity that the probable magnitude of resultant and undetectable errors can never be predicted. This is clearly unsatisfactory and underlines the value of long-term studies which enable the worker to study the formation of annuli and other scale checks over a period of many years. It is only from such studies that basic improvements in technique and interpretation can be made.

ACKNOWLEDGEMENTS

The work described in this paper formed part of a larger project financed by the Natural Environment Research Council and the Warrington Anglers Association. To both of these bodies I am very grateful. I am also indebted to Dr. J. W. Jones, O.B.E., for supervision of the work; Mr. T. B. Bagenal, for assistance in the preparation of slides and scale photographs; and to the Board of Glamorgan River Authority for permitting me to present the paper at the Symposium.

REFERENCES

- Banks, J. W. (1970). Observations on the fish population of Rostherne Mere, Cheshire. *Field Studies*, **3**, 357-379.

- Cragg-Hine, D. (1965). Age determination in coarse fish. Proc. 2nd Brit. Coarse Fish Conf., 3-6.
- Cragg-Hine, D., and Jones, J. W. (1969). The growth of dace *Leuciscus leuciscus* (L.), roach *Rutilus rutilus* (L.) and chub *Squalius cephalus* (L.) in Willow Brook, Northamptonshire. J. Fish Biol., 1, 59-82.
- Hartley, P. H. T. (1947). The natural history of some British freshwater fishes. Proc. Zool. Soc. Lond., 117, 129-206.
- Jones, J. W. (1953). Part I. The scales of roach. Part II. The age and growth of the trout (*Salmo trutta*), grayling (*Thymallus thymallus*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*) of Llyn Tegid (Bala) and the roach of the River Birket. Fishery Invest., Lond. (I), 5, (7), 1-18.
- Karpinska-Walus, B. (1961). The growth of roach (*Rutilus rutilus* L.) in lakes of Wegorzewo District. Roczn. Nauk. Roln., 77-B-2, 329-398.
- Le Cren, E. D. (1947). The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. J. Anim. Ecol., 16, 188-204.
- Linfield, R. S. J. (1971). Observations relating to problems of fishery management at Grey Mist Mere. Proc. 5th Brit. Coarse Fish Conf., 78-88.
- Linfield, R. S. J. (1973). Fishery studies at Grey Mist Mere. Proc. 6th Brit. Coarse Fish Conf., 166-173.
- Masterman, A. T. (1923). Report on the scales of certain freshwater fish in relation to age determination. Fishery Invest., Lond., (I), 1, (3), 1-16.
- Seegerstrale, C. (1932). Über die jährlichen Zuwachszonen der Schuppen und Beziehungen zwischen Sommer-Temperatur und Zuwachs bei *Abramis brama*. Act. Zool. Fenn., 13, 1-42.
- Von Bertalanffy, L. (1938). A quantitative theory of organic growth (Inquiries on growth laws II). Human Biol., 10, (2), 181-213.
- Walford, L. A. (1946). A new graphic method of describing the growth of animals. Biol. Bull. Mar. Biol. Lab. Woods Hole, 90, 141-147.
- Wallin, O. (1957). On the growth structure and developmental physiology of the scale of fishes. Rept. Inst. Freshwat. Res. Drottningholm, 38, 385-447.
- Williams, W. P. (1967). The growth and mortality of four species of fish in the River Thames at Reading. J. Anim. Ecol., 36, 695-720.