FISH PRODUCTION IN RIVERS UNDER HUMAN IMPACT

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SUMMARY

The measurement of fish production is potentially a useful tool in fishery management. Not only can it be used to assess the impact of environmental change on the well-being of a population, but it can lead to an estimate of the optimum harvest (or yield) for a particular fishery. But the successful application of production information depends greatly on the accuracy of the component data, especially population density. Gross errors in these quantitative estimates can result in ill-advised management regimes.

Relatively few of the papers examined in this review deal directly with the effects of habitat change, and those that do are confined largely to studies of salmonid-dominated fish communities. Most other investigations may be classed as fundamental research projects designed to advance our knowledge of fish population dynamics, and to provide a firm ecological basis for future fishery management.

The mechanisms controlling the levels of fish production in rivers are still poorly understood (MAHON, BALON, 1985). Abiotic factors, especially floods, appear to determine population densities in many head-water habitats (CRISP et al., 1974, 1975; WATERS, 1983; PENCZAK, MOLINSKI, 1984). But the potential maximum production in such waters may be under biotic control (MAHON, BALON, 1985; ZALEWSKI, NAIMAN, 1985), chiefly through the levels of autochthonous and allochthonous food resources, which regulate growth rates (STATZNER, HIGLER, 1985); though even these variables may be under abiotic influence (WATERS, 1983; ZALEWSKI, NAIMAN, 1985). Hence the density-dependent regulating mechanisms for salmonids, often apparent in more productive waters, are rarely brought into play because population densities are not sufficiently high. Where they operate in more stable environments, then cover for fish (plants, stones) can play a major role in setting the levels of population density.

Fish production data (in the Ivlev sense) have much potential in fishery management, especially in assessing the impact of environmental perturbations or in determining optimum fish harvests. But the component parameters require accurate

te estimation in order to predict the outcome of a particular management regime with any confidence. Errors in riverine studies can arise from the variability of habitats along the river continuum (STATZNER, HIGLER, 1985; ZALEWSKI, NAIMAN, 1985) unless sampling sites are chosen with sufficient care to avoid fish species composition or age-structures to be misrepresented in the samples.

Productivity levels are under both biotic and abiotic influence, with the latter being of prime importance in many upland waters. Biotic variables (cover, food, predation) have more influence in stable environments, although physical parameters, especially water temperature, can still play a major role in determining the characteristics of local fish populations.

Salmonid studies dominate the literature; but as yet we know little about the dynamics of non-salmonid populations. We would encourage more studies on the latter, particularly of the O group fish.

INTRODUCTION

To begin the title of this paper it is necessary to explain that there are no restraints in its contents. We would like to underline that pristine rivers are almost nonexistent phenomenon nowadays (HORWITZ, 1978; SEDELL, LUCHESSA, 1982; STATZNER, HIGLER, 1985). We suppose that main source of limitations so as to explain the relationships between production values and abiotic and biotic factors are connected with unknown precise human impact extended to the investigated river.

The International Biological Programme provided a useful stimulus to production studies at all trophic levels and led, directly or indirectly, to several review articles pertaining to fish (CHAPMAN, 1967, 1978; WATERS, 1977; MORGAN et al., 1980; NEVES, 1981). Despite all this activity, it was noted by MORGAN et al. (1980) that factual information on basic parameters such as mean biomass and production was sparse. The above reviews embrace both lacustrine and riverine studies, but in our paper we concentrate on the problems associated with flowing-waters. In particular we examine the constraints that such habitats impose upon the estimation of fish production, and we discuss the factors which determine productivity levels.

DEFINITION

Despite the efforts of many writers (e.g. CHAPMAN, 1967; WATERS, 1977) there is still confusion in the literature over the use of the term "production". In this paper we use production in the IVLEV (1945) sense: Production is the total quantity of tissue elaborated by a fish population during a stated period of time, even though not all of it may survive to the end of that time.

As production as a synthesis of population biomass, recruitment and the instantaneous rates of growth and mortality, it is especially responsive to the welfare of the population and to the effects of environmental change. However, production does not indicate fully the importance of a particular group of animals (e.g. cohort, population) in terms of energy turnover, although such information may be acquired via production estimates (ALLEN, 1951;

TABLE I.- Range of production (P) estimates and turnover ratio (P/B) for non-salmonid fishes in North American rivers.

SPECIES	P(g m ⁻² yr ⁻¹)	No. of estimates	P/B	No. of estimates
Ambloplites rupestris	0.03-0.24	2	1.13	1
Campostoma anomalum	0.89-1.36	2		
Catastomus commersoni	0.14-4.20	2	2.03-3.92	2
Clinostomus funduloides	0.07	1		
Cottus bairdi	0.82	1		
C. carolinae	4.25	1		
C. cognatus	5.94	1	1.20	1
Cyprinodon nevadensis	155.40*	1	5.00	1
Etheostoma caeruleum	0.06-0.63	3	1.33	1
E. flavellare	0.02-1.65	6	1.35-2.36	1
E. nigrum	0.06-0.36	3	3.01	1
E. sagitta	0.06-0.42	2		
E. spectabile	2.65	1		
Ericymba buccata	0.16	1		
Hypentelium nigricans	0.64-5.48	2	1.30-1.97	2
Micropterus dolomieu	0.01-0.05	2	7.53	1
Moxostoma rhothoecum	0.54	1		
Nocomis leptcephalus	0.11	1		
Notropis chrysocephalus	0.17	1		
N. cornutus	0.30-1.99	2	2.07-3.10	2
Pimephales notatus	0.38-1.36	3	2.79-3.10	3
Prospium williamsoni	5.31	1		
Rhinichthys atratulus	0.32-0.36	3	2.39-2.50	2
R. cataractae	0.10-0.86	3	2.22-2.92	2
Semotilus atromaculatus	0.81-9.26	5	1.05-2.48	5
Mean (+95% conf. limits)	1.56 (+0.85)		3.01 (+1.25)	

data from: GOODNIGHT, BJORN, 1971; LOTRICH, 1973; SMALL, 1975; PETROVSKY, WATERS, NAIMAN, 1976; MAHON et al., 1979; HALYK, BALON, 1983; NEVES, PARDUE, 1983; PENCZAK, MAHON, BALON, 1984).

* not included in the mean value.

WARREN et al., 1964; MAN, 1982, 1983).

Production, as defined above, should not be confused with "yield", although the two words are sometimes treated as synonyms. In fishery terms, yield is that part of the annual production of a population that is cropped by man, or moves from one habitat to another (as in the migration of Salmo salar smolts to the sea). Thus yield is dependent upon the level of production and, in a fishery, on the degree of fishing effort. Conversely, a high fishery yield (hence a high fishing mortality) may affect subsequent production by reducing the number of larger, older fish, as occurred with Barbus callensis in an Algerian river (PENCZAK, MOLINSKI, 1984).

Note that production is rate; it is expressed as weight (or energy) per unit area per unit time.

Presentation of methods how to measure of production and its components (density, mortality, fecundity, instantaneous growth rate, body length

TABLE II.- Range of production (P) estimates and turnover ratio (P/B) for salmonid fishes in rivers.

SPECIES	P(g m ⁻² yr ⁻¹)	No. of estimates	P/B	No. of estimates
<i>Salmo clarki</i>	3.50- 4.90	3	0.87-1.06	3
<i>S. gairdneri</i>	1.30-13.20	4	1.49	1
<i>S. salar</i>	0.22-11.00	16	1.41	2
<i>S. trutta</i>	0.11-54.70	53	0.48-2.70	37
<i>S. alpinus</i>	0.01- 2.22	8		
<i>S. fontinalis</i>	0.64-30.00	11	0.71-2.54	9
<i>Oncorhynchus kisutsch</i>	8.00	3		
<i>O. tschwytscha</i>	0.60- 2.51	2		
Means ($\pm$ 95% conf. limits)	9.65 ($\pm$ 3.05)		1.57 ($\pm$ 0.31)	

data from: ALLEN, 1951; HORTON, 1961; HORTON et al., 1968; CHAPMAN, 1965, 1966; LOWRY, 1966; COOPER, SCHERER, 1967; LIBOSVARSKY, 1968, 1971; HUNT, 1969, 1974; Le CREN, 1969; ELWOOD, WATERS, 1969; LUSK, ZDAZILEK, 1969; EGGLISHAW, 1970; LIBOSVARSKY, LUSK, 1970; HOPKINS, 1971; MAN, 1971; POWER, 1973; ALAKSANDER, MacCRIMON, 1974; CRISP et al., 1974, 1975; HANSON, WATERS, 1974; MORTENSEN, 1977, 1982; EGGLISHAW, SHACKLEY, 1977; CRISP, CUBBY, 1978; MILNER, et al., 1978; O'CONNOR, POWER, 1976; WATERS, 1982, 1983; WITWORTH, STRANGE, 1983; LOBON-CERVIA, PENCZAK, 1984; PENCZAK et al., 1985; LOBON-CERVIA et al., 1986.

and body weight at time of annulus formation and so on) is not indispensable for the limnologists and ecologists. We consider that we should be mainly concentrating on factors which are limiting our investigations in rivers.

We believe that it is not difficult to investigate the fish production value at site in small, lowland, alluvial rivers. In such rivers with limited hiding places, reduced to small clumps of macrophytes, we can conduct almost total catch (PENCZAK, 1981). But accuracy of a sampling and its credibility is inversely correlated with river size. Not everyone remembers about the inexorable pressure of the truth included in this statement and makes attempt at assessing fish stock in bigger and bigger rivers. Such obstinate enthusiasts may sometime, however, contribute to the development of knowledge.

In rivers whose water levels fluctuate widely there is a difficulty in assessing stream area. LOTRICH (1973) suggested that stream length may be more useful than area as the basis for appraising or comparing the dynamics of intermittent streams. However, he used minimum stream area on which to base his production estimates, as have other involved with streams with a variable discharge (CRISP, et al., 1974, 1975; PENCZAK, MOLINSKY, 1984). The latter authors observed a ten-fold difference in the production level of fish in a seasonal river in north Algeria, depending on whether minimum or maximum stream area was used in the computation.

REVIEW OF THE LITERATURE

The range of production estimates and turnover ratios (P/B) for salmonid fishes world-wide and for non salmonids in Europe and North America are shown in Tables I-III. Few data were found for rivers outside Europe and North

TABLE III.- Range of production (P) estimates and turnover ratio (P/B) for non-salmonids fishes in European rivers.

SPECIES	P(g m ⁻² yr ⁻¹)	No. of estimates	P/B	No. of estimates
<i>Abramis brama</i>	0.15	1		
<i>Alburnus alburnus</i>	52.80	1	1.62	1
<i>Alburnoides b. strimonicus</i>	0.03- 0.12	3	1.23	3
<i>Anguilla anguilla</i>	0.09- 9.30	5	0.57-1.73	3
<i>Aspius aspius</i>	0.15	1	0.49	1
<i>Barbus barbus</i>	0.60- 0.43	2	1.87	1
<i>B. cyclolepis</i>	0.50- 5.61	5	1.10	5
<i>B. b. bocagei</i>	0.23-17.50	5	0.30-1.44	5
<i>Blicca bjoerkna</i>	0.01	1		
<i>Chondrostoma nasus</i>	0.01- 0.95	2	0.20	1
<i>C. polylepis</i>	1.59-10.01	6	0.56-1.72	6
<i>Cobitis paludicola</i>	0.14	1	1.98	1
<i>Cottus gobio</i>	0.40-43.10	12	1.33-3.19	3
<i>Exox lucius</i>	0.15- 0.52	5	0.67-1.16	4
<i>Gasterosteus aculeatus</i>	0.10-42.30	7	0.90-3.70	5
<i>Gobio gobio</i>	0.03-11.70	11	1.00-2.86	11
<i>Leucaspis delineatus</i>	0.09	1	2.25	1
<i>Leuciscus cephalus</i>	0.01- 9.40	12	0.28-2.03	12
<i>L. leuciscus</i>	0.23- 2.60	3	0.37-1.75	3
<i>Lota lota</i>	0.01	1		
<i>Noemacheilus barbatulus</i>	0.10-17.35	6	0.21-1.90	2
<i>N. bureschi</i>	0.01-2.31	3	1.32	3
<i>Perca fluviatilis</i>	0.01- 2.03	3	0.30	1
<i>Phoxinus phoxinus</i>	0.01- 3.90	9	1.90-2.00	9
<i>Pungitius pungitius</i>	1.80	1	0.61	1
<i>Rutilus rutilus</i>	0.20-17.80	4	0.32-1.14	3
<i>R. arcasii</i>	0.03- 1.55	5	1.71-2.30	5
<i>Silurus glanis</i>	0.02	1	0.35	1
<i>Stizostedion lucioperca</i>	0.09	1	0.66	1
Mean (+95% conf. limits)	5.89±2.86		1.32±0.42	

data from': BACKIEL, 1970, 1971; MATHEWS, 1970,1970; Le CREN, 1962; CRISP, et al., 1974, 1975, 1984; LIND, KAUORANT, 1975, MANN, 1971,1980; PENCZAK et al., 1976,1982, PHILIPPART, 1977, 1981; RAMUSSEN, THERKILDSEN, 1979; PENCZAK, 1981; PENCZAK et al., 1985; KICKLEY, BAILEY, 1982; LOBON-CERVIA, PENCZAK, 1984 MANN, PENCZAK, 1984; PENCZAK, MOLINSKI, 1984; LOBON-CERVIA et al., 1986; O'HARA, PENCZAK, 1987.

America, notable exceptions being the studies by ALLEN (1951) and HOPKINS (1971) in New Zealand, and by BISHOP (1973) in small Malayan river in which estimates of 36 to 90 g m⁻² yr⁻¹ for the whole fish community were obtained using the model described by HUET (1964), and by WATSON, BALON (1984) in rain forest stream of northern Borneo where estimates of 26.1 to 261.5 g m⁻² yr⁻¹ (mean: 76.7) for the all populations.

The highest estimate for single species is 155.4 g m⁻² yr⁻¹ for the Armagosa pupfish, *Cyprinodon nevadensis*, a short-lived herbivore living in a warmwater spring (28-34°C) and subject to year-round growth conditions (NAIMAN, 1976). Other high estimates are 54.7 for *Salmo trutta* (ALLEN, 1951), 52.8 for

FIGURE 1

Frequency-distribution (%) of production estimates for non-salmonid fishes in North America (N = 48) and Europe (N = 118), and salmonid fishes world-wide (N = 100).

the small cyprinid Alburnus alburnus in the river Thames (MATHEWS, 1970, 1971) 43.1 for the sculpin, Cottus gobio in a small chalkstream in southern England (MANN, 1971), and 74.0 for stone loach, Noemacheilus barbatulus in the upper course of the Utrata River, Poland (PENCZAK, 1981).

For stream salmonids, Le CREN (1969) suggested that there was an upper production limit of 12 g m⁻²yr⁻¹. Subsequent studies have indicated the ceiling to approximate 30 g m⁻²yr⁻¹, and the frequency distribution (Fig. 1) shows that only four estimates equalled or exceeded this value; viz. 54.7 (ALLEN, 1951), 46.2 (LOBON-CERVIA et al., 1986), and 33.1 (MORTENSEN, 1982) for S. trutta and 30.0 for Salvelinus fontinalis in Big Spring, Pennsylvania (COOPER, SCHERER, 1967).

More studies of salmonid production have been made than for any other group of fishes. ALLEN's (1951) high rate is often considered to be an overestimate, but COOPER, SCHERER (1967) point out that ALLEN's population

estimates are similar to those for S. fontinalis in Big Spring, but the S. trutta grew very much faster. They argued that this faster growth is sufficient to explain the high trout production in the Horokiwi Stream.

The pronounced effect that local environmental conditions have on the level of fish production, particularly in relation to fish cover, was highlighted by CHAPMAN (1966). Later, HUNT (1969) demonstrated the effect experimentally; following habitat improvements in Lawrende Creek, Wisconsin he recorded an increase from 3.7 to 16.7 g m⁻²yr⁻¹ in the production of S. fontinalis. Natural variations in relation to habitat structure were recorded also for S. trutta and C. gobio in a small stream in southern England (MANN, 1971, 1983). Lower densities of both species were found in a heavily-shaded section than in an adjacent open containing many submerged macrophytes. No difference in growth rate were observed, but EGGLESHAW, SHACKLEY (1977) found the environmental factors influenced the population densities of S. trutta and S. salar in a Scottish stream, and that growth rates were inversely proportional to population density. In many Norwegian rivers, the species S. trutta, S. salar and Salvelinus alpinus are segregated according to substrate type (POWER, 1973). Also, the presence of cover in the form of boulders and large stones greatly enhances the holding capacity of the rivers for fish, and hence influences the production level.

A beneficial change as a result of man's activities was described by CRISP et al., (1984). The production of juvenile S. trutta in small moorland streams increased after the main river into which they flowed had been impounded to form a reservoir. An increase in the recruitment was related to an increased size of adults spawning in the tributaries (hence more eggs were laid) and to a deeper cutting of the redds by the larger adults (hence more eggs survived the effects of floods). The release of cold hypolimnetic water from a new impoundment prevented the successful spawning of the previously abundant species Rhinichthys atratulus and Etheostoma flabellare (PENCZAK, et al., 1984). These two species plus four less common ones were replaced by three new species in the study area and, despite lower water temperatures, total annual production was tripled.

Geographic variation in the production of individual species, related to the basic productivity of the streams, has been recorded widely (COOPER, SCHERER, 1967; CRISP et al., 1974, 1975), and it is supported by the results of the enrichment of experimental streams with sucrose (WARREN, et al., 1964).

ALLEN (1969) suggested that natural selection, operating through the influence of environmental factors on individuals in two isolated populations, could result in genetic differentiation between the two groups. However a reciprocal transfer of C. gobio between two very different habitats resulted in the transferred sculpins assuming the growth and reproductive characteristics of the local population (MANN et al., 1984). In this example, at least, the genotype appeared capable of a wide range of phenotypic expression, with the characteristics of a specific population being determined by local conditions. Such plasticity of life-history tactics may underlie the successful establishment of many temperate species into a wide range of habitats (MANN, et al., 1984).

As it was mentioned in the chapter "Definition", the open-ended nature of rivers can pose problems in the study areas. By studying review work devoted to the assessment of fish stocks in rivers one can easily see that this difficult and time-consuming task has become a serious limitation in ecological theory. To minimize the obstacle, ichthyologists have examined and analysed many parameters influencing sampling and the accuracy of assessing density and standing crop, e.g. sampling time, sampling techniques, gear, behaviour

of sampled animals, the use of environmental parameters, etc. (ZALEWSKY, 1986). However, the length of the river section used for sampling has not always been taken into account (PENCZAK, 1985). Consequently, the actual choice of site has not been a subject of investigation, and thus has been determined from arbitrary decisions. Only the homogenous structure of the section for sampling and the representation of the site for the investigated river section have been considered (PENCZAK, 1985); at the most it has been observed that when "the small species were numerous" it was sufficient to fish a shorter section of the river (WILLIAMS, HARCUP, 1974).

So far the importance of the choice of the river section, for the optimal density assessment, has been fully recognized and substantiated only for plant studies, immobile invertebrates and large mammals.

In the case of large rivers, the problem of the choice of site is important because most of the qualitative and quantitative composition of ichthyofauna fluctuates commutatively along the whole course. The production of transitory fish can be estimated for the period they remain in the study area, provided that the frequency of sampling is adequate. But some data concerning fish movements, and more widespread sampling, are necessary if status of the whole (biological) populations is required. CRISP et al. (1974, 1975) tackled this problem by combining an intensive study of a few, selected sites with a more general survey of many sites over whole of catchment. Although the sampling regime was compromise between logistics and scientific requirements, combination of the two sets of data led to a realistic evaluation of fish production.

Because we gathered considerable amount of data on the turnover ratio (Table I-III) we would like to reveal a fact that no all investigators are using average biomass ($\bar{B}$) for calculation of production for no directly investigated species ("other species"). WATERS (1977) proposed the use of maximum biomass (B_{max}) instead of B , but we found no examples of its use in estimating fish production - possibly because B_{max} is more difficult to determine from field data than is $\bar{B}$. ALLEN (1971) noted that both mean age and mean life-span are reciprocals of the $P/\bar{B}$ ratio if there is constant exponential mortality, a point also demonstrated by LEVÊQUE (1978). Later, BANSE, MOSHER, (1980) examined the relationship between $P/\bar{B}$ and mean body weight at maturity; they found linear log:log relationships for several groups of animals including fish. However, more accurate data on $P/\bar{B}$ ratios are required for many fish species before any of these relationships can be used to determine production levels accurately, although the information for salmonids is approaching this position.

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