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Comparison of age-structured and length-converted catch curves of brown trout *Salmo trutta* in two French rivers

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Abstract

Age-structured catch curves (ACC) and two different types of length-converted catch curves (LCC), covering the same size/age range of trout *Salmo trutta* (Pisces: Salmonidae) in two French rivers, were used to estimate total mortality (Z). It is shown that standard LCC overestimate Z when ACC are used as controls, while LCC explicitly considering seasonal growth oscillations produce unbiased estimates. The implications of this finding for length-based fish stock assessment are discussed.

Keywords: Age distribution; Length distribution; Mortality; *Salmo trutta*

1. Introduction

Numerous methods of estimation of total mortality (Z) in fish populations are now available and have been discussed in various reviews (Ricker, 1975; Gulland, 1983; Pauly, 1984; Pauly and Morgan, 1987). Of these, length-converted catch curves (LCC) are probably most straightforward. However, simulation studies conducted by Hampton and Majkowski (1987) suggest that LCC tend to overestimate total mortality (Z). They write: "growth parameter variation [...] was the cause for the large positive bias [of Z]. There is no obvious reason why this should be so; further work is required to resolve this question." Similar re-

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sults were obtained by Isaac (1990), while Sparre (1990) showed that seasonal growth is one of the causes for this bias. This present paper, building on Pauly (1990), presents a method by which this bias can be overcome.

This method is illustrated by comparing total mortality estimates obtained by age-structured catch curves and two versions of length-converted catch curves, using data for *Salmo trutta* populations in two French rivers. These results are discussed in the light of the above-mentioned bias.

2. Materials and methods

Trout were sampled by electrofishing (Abad, 1982; Moreau and Abad, 1987) in two French salmonid rivers, the Viau and the Vèbre in the southern part of the Massif Central.

Samples were taken from each river in August 1979, November 1979, February 1980 and May 1980 (Tables 1 and 2). The age groups (Table 1) were obtained from the samples in Table 2, wherein the ages are based on scalimetry of individual fish (Abad, 1982). The growth parameters of trout used here are given in Table 3.

Based on the four samples obtained from each river, total mortality (Z) was estimated from the slope of the descending straight segment of the catch curves described below; these segments all cover similar ranges of fish sizes, but do not include the same number of points, as the aggregation was different in each case.

2.1. Age-structured catch curves (ACC)

As for all catch curve analyses, recruitment was assumed to be constant, or to have varied only little, and without trend for several years prior to sampling (Ricker, 1975). Total mortality was estimated from:

$$\log_e(N_i) = a + bt_i \quad (1)$$

where N is the number of fish of age t , a and b are estimated through regression analysis and b , with sign changed, is an estimate of Z (note that ACC serves here as 'control').

2.2. Standard length-converted catch curves (LCC1)

Here, estimates of Z were obtained under the same assumption concerning recruitment for each river, from the summation of all four 'seasonal samples' in Table 2 (referred to as the 'annual sample'). Total mortality was estimated from:

$$\log_e(N/t_i) = a + bt_i \quad (2)$$

where N , a , b and t_i are as defined above and where t_i is the time needed for the fish of a given length class i to grow through that length class (Gulland, 1983).

Table 1
 Number of trout sampled, by age, season in the Viau ($n=6038$) and Vèbre ($n=3556$) (adapted from Abad (1982))

Age (years)	Sampling dates	Number of fishes, by river	
		Viau	Vèbre
0.25	15/5/80	601	129
0.50	15/8/79	582	73
0.75	15/11/79	643	121
1.00	15/2/80	496	127
1.25	15/5/80	405	283
1.50	15/8/79	392	370
1.75	15/11/79	298	294
2.00	15/2/80	389	371
2.25	15/5/80	312	318
2.50	15/8/79	300	378
2.75	15/11/79	314	250
3.00	15/2/80	345	348
3.25	15/5/80	115	124
3.50	15/8/79	120	86
3.75	15/11/79	162	47
4.00	15/2/80	151	76
4.25	15/5/80	49	40
4.50	15/8/79	37	23
4.75	15/11/79	80	14
5.00	15/2/80	62	28
5.25	15/5/80	19	11
5.50	15/8/79	21	14
5.75	15/11/79	38	6
6.00	15/2/80	34	6
6.25	15/5/80	12	8
6.50	15/8/79	13	6
6.75	15/11/79	9	0
7.00	15/2/80	16	0
7.25	15/5/80	7	3
7.50	15/8/79	6	2
7.75	15/11/79	6	–
8.00	15/2/80	4	–

Given the set of von Bertalanffy growth parameters in Table 3, t values were obtained from:

$$t_i = -1/K \log_e [(L_\infty - L_{2i}) / (L_\infty - L_{1i})] + t_0 \quad (3)$$

where L_{1i} and L_{2i} are the lower and upper limits, respectively, of length class i (Pauly, 1984).

2.3. Seasonal length-converted catch curves (LCC2)

The same length-frequency samples were used as described above for LCC1 (Table 2), but they were analysed using the method of Pauly (1990), i.e. by sum-

Table 2

Seasonal length–frequency distributions in the trout populations in the Viau ($n=6038$) and the Vèbre ($n=3556$) (from Abad (1982))

LT (cm)	Viau ^a				Vèbre ^a			
	1	2	3	4	1	2	3	4
4	30			47				
5	128	6		158				
6	245	60	63	224	18			40
7	139	171	87	135	40	2	2	62
8	39	227	189	34	14	40	42	22
9	0	120	121	0	1	53	60	5
10	0	34	36	0	5	24	23	3
11	30	0	0	38	30	2	5	18
12	78	12	15	98	93	13	11	70
13	135	48	68	127	122	50	60	104
14	113	104	129	106	91	94	131	68
15	65	101	120	61	45	106	122	31
16	78	65	65	77	78	49	57	59
17	114	75	81	120	109	47	55	99
18	63	114	132	72	110	89	111	86
19	23	67	75	29	67	56	101	60
20	39	65	67	27	37	39	59	46
21	46	37	31	39	30	13	28	59
22	18	57	56	28	18	26	32	23
23	18	32	33	14	8	11	23	11
24	9	24	20	12	7	2	9	24
25	13	18	16	15	7	8	13	4
26	7	29	20	12	5	4	6	3
27	2	21	15	11	5	1	2	5
28	7	13	14	3	4	2	3	2
29	5	11	9	7	2	0	0	3
30	8	12	9	3	3	1	1	3
31	5	5	8	3	1			2
32	2	5	5	5	2			3
33	2	2	5	2				1
34	1	3	2	3				
35	2	1	3	1				
36	1	1	1	3				
37	2	2	1	2				
38	1	1	1	1				
39	1	3		1				
40	1	1		1				
41	1	1		1				
42		2						
Total	1471	1550	1497	1520	952	732	956	916

^a 1, 2, 3 and 4 refer to August 1979, November 1979, February 1980 and May 1980, respectively.

Table 3
Von Bertalanffy growth parameters estimates for two French trout populations (Abad, 1982)

River	L_{∞} (cm, TL)	K (1/year)	t_0 (years)
Viau	70.8	0.087	-0.67
Vèbre	45.9	0.161	-0.38

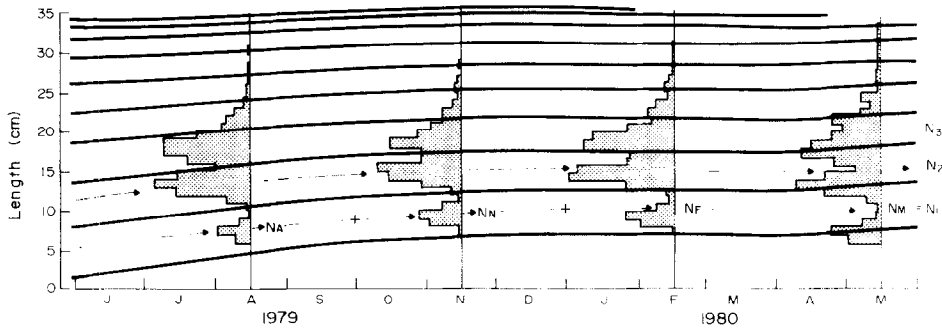


Fig. 1. Schematic representation of method used to 'slice' length-frequency samples (here: Vèbre River, from Table 2) using the previously estimated parameters of a seasonally oscillating growth curve. The method cumulates the number of fish within the pseudo-cohorts (e.g., $N_{\text{August}} + N_{\text{November}} + N_{\text{February}} + N_{\text{May}}$), as obtained by 'slicing', and uses these as estimates of N_i to construct a length-converted catch curve which explicitly accounts for seasonal growth oscillations. (This representation, showing only ten 'slices', is schematic in that the GOTCHA program performs the computation actually using a number of slices similar to the number of length classes, to facilitate comparison between LCC1 and LCC2; see Fig. 2.)

Table 4
Monthly changes in water temperature ($^{\circ}\text{C}$), in 1979, for the two rivers

River	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Viau	4.5	7.0	8.5	10.7	11.5	13.5	14.5	16.5	12.5	8.0	6.8	6.0
Vèbre	5.3	6.5	7.2	8.3	10.5	12.0	13.5	15.5	12.5	9.5	7.5	6.3

ming the number of fish within 'slices' cut by successive growth curves, as illustrated in Fig. 1. The actual computations were performed using the GOTCHA software of Gayanilo (1991), which includes the approach in Fig. 1 as a separate routine. Note that this approach requires growth parameters to be available beforehand, i.e. it is not used to estimate growth parameters.

This routine, now also incorporated in the FISAT software (Gayanilo et al., 1994), assumes that a seasonally oscillating version of the von Bertalanffy equation is used to describe the growth in length of the fish studied; specifically, it uses Somers' (1988) modification of the seasonal growth model of Pauly and Gaschütz (1979):

$$L_t = L_\infty (1 - \exp\{-[K(t - t_0) + S(t) - S(t_0)]\}) \tag{4}$$

where L_t is the length at age t , L_∞ the mean length of the fish would reach if they were to grow indefinitely, K is the von Bertalanffy curvature parameter, t_0 the theoretical age at which length is zero, where $S(t) = (CK/2\pi)\sin 2\pi(t - t_s)$, $S(t_0) = (CK/2\pi)\sin 2\pi(t_0 - t_s)$, and C and t_s describe the amplitude and timing, respectively, of the seasonal growth oscillations. Note that this equation reduces to the standard von Bertalanffy model, $L_t = L_\infty (1 - \exp\{-[K(t - t_0)]\})$, when $C = 0$.

As estimates of C and t_s were not available for the trout studied here, we have assumed a value of $C = 1$, leading to a complete growth stop in winter (as suggested by clear annual rings on the scales (Abad, 1982)), and to a growth rate $dl/dt = 0$ during a very short winter period. Further, we have set $t_s = 0.583$, corresponding to a winter point (WP = $t_s + 0.5$) set at the end of January, when temperatures are lowest (Table 4). While seasonal growth must occur for the conclusions below to hold, the exact values of C and t_s are not critical to these conclusions (see simulations by Sparre (1990)).

3. Results and discussion

Fig. 2 presents the catch curves and the estimates of Z obtained, by river and catch curve type. As can be seen, the Z values obtained from LCC1 are markedly

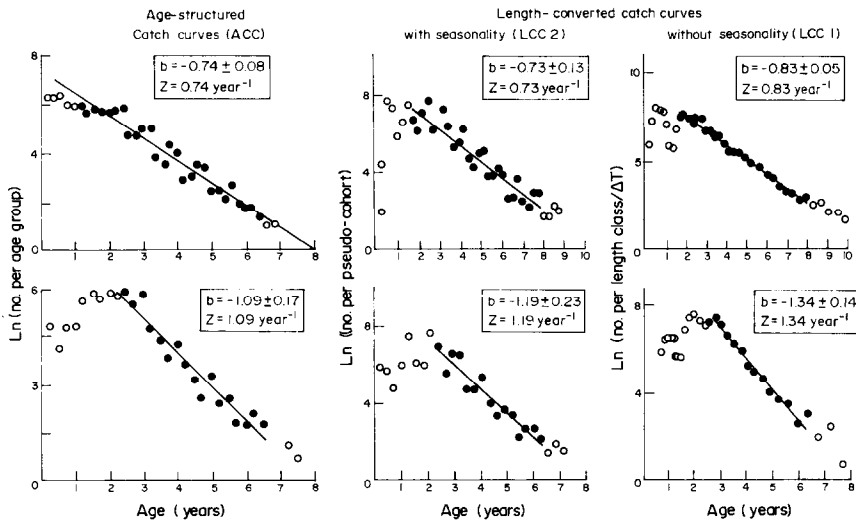


Fig. 2. Estimates of total mortality (Z , 1/year) of trout in the Viau and Vèbre rivers, France, obtained from three different types of catch curves. The full dots cover the same range of sizes for each river (above, Viau; below, Vèbre). Note match of estimates between ACC and LCC2, and overestimation by LCC1 (see also text).

higher than Z estimates based on ACC used here as control, the overall bias being of the same order as in the simulations of Hampton and Majkowski (1987).

On the other hand, the LCC2 provided in one case an estimate that was equal to, in the other case only slightly higher than, the ACC estimate. Note, however, that we refrain here from conducting formal parametric tests (e.g. t -tests for difference of slopes) because (1) the confidence interval (CI) of the slope is not equivalent to the CI of Z , since the latter is estimated from points selected to lie on the straight descending arm of the catch curves, and (2) the CI of the slopes are in any case too wide relative to the magnitude of the bias discussed here.

Sparre (1990) and Pauly (1990) showed this bias to be very strong in short-lived animals such as penaeid shrimps with strong growth oscillation, i.e. $C \approx 1$ in Eq. (4). Fig. 2, on the other hand, confirms Pauly (1990) to the effect that this bias can be completely overcome when using an LCC2-type catch curve—even in cases of slow-growing fishes such as trout, where the bias is small.

This suggests that it may be superfluous to split length composition data into age groups if one's aim is solely to construct a catch curve to estimate Z . Rather, an LCC2-type catch curve can be constructed directly. The resulting estimate of Z will not be biased by the effect of seasonal growth, as this catch curve type explicitly takes seasonal growth into account.

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