

Downstream displacement of post-emergent brown trout: effects of development stage and water velocity

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Brown trout *Salmo trutta* were introduced at hatching into distinct sections of two parallel artificial channels, one with a constant low velocity (control) and one with velocity changes (experimental), at such times as to produce 12, 3 and 0 day old fish (age after emergences) when the velocity was changed in the experimental channel. This experimental design was repeated in 2002 and 2003 at comparable dates. Young brown trout were sensitive to an increased water velocity for 5 to 6 days after emergence. Water velocity modified the displacement patterns qualitatively but not quantitatively. Eighty per cent of fish moved downstream at all water velocities. Velocity changes, however, advanced the time by which 80% of the fish had displaced downstream.

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Key words: brown trout; downstream displacement; emergence; stage of development; water velocity.

INTRODUCTION

As early stages of development are particularly sensitive to biotic and abiotic constraints, studying these stages in terms of survival is essential in population ecology. In the particular context of stream ecosystems, salmonids, and especially brown trout *Salmo trutta* L., have received considerable attention relative to other fish groups. Several studies showed that high flows in winter and spring reduce young-of-the-year (YOY) brown trout density (Allen, 1951; Spina, 2001; Cattaneo *et al.*, 2002), especially if high flows occurred during emergence (Allen, 1951; Nehring & Anderson, 1993; Nuhfer *et al.*, 1994; Latterell *et al.*, 1998; Liebig *et al.*, 1999). The mechanisms by which high flows during emergence influence YOY losses, however, are still unclear.

In brown trout, a first phase of downstream displacement occurs immediately after emergence (Huet, 1961; Elliott, 1966; Timmermans, 1966). As a first step in the understanding of YOY losses under high discharge conditions, some authors studied the influence of water velocity (hereafter called velocity) on such displacements. Ottaway & Clarke (1981) and Crisp & Hurley (1991a)

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experimentally submitted emerging brown trout to velocity changes. They observed a positive relationship between displacement rate and velocity. The strength of the relation seemed to depend on the stage of fish development. Fish were introduced, however, directly into the experimental channels without emerging naturally from the gravel and some experiments were performed pooling fish at different stages of development (Crisp & Hurley, 1991a). As a consequence, the critical stage of development affected by velocity in terms of the number of days since emergence could not be defined.

In further experiments, Ottaway & Forrest (1983) and Crisp (1991) dealt with this difficulty by introducing fish long before emergence in different channels. In each channel, the velocity was set at different but constant values. Displacement mainly occurred when young brown trout entered the free-feeding stage and the rate of displacement was higher at high than at low velocities. The final density was similar at all velocities (Crisp, 1991) but was approached more and more rapidly as velocity increased.

These experiments were useful contributions in determining the stage of development that was most sensitive to velocity. Fish, however, were submitted to constant velocity conditions. In a final experiment, Crisp & Hurley (1991b) showed that changes in velocity (from high to low or low to high) were associated with a higher displacement rate than under constant velocity conditions. Therefore, further experiments seemed essential to determine the stage of development most sensitive to changes in velocity conditions. In this present study, the simultaneous influence of velocity changes on the downstream displacement of brown trout groups at different stages (0, 3 and 12 days after emergence) was studied in an artificial flume. The experimental design included controls, involved fish emerging *in situ* and was repeated in comparable periods in 2002 and 2003. The latter consideration meant experiments could be repeated under comparable night duration, which is known to influence salmonid downstream displacement (Crisp, 1991; Bardonnnet *et al.*, 1993).

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

The simultaneous influence of water velocity changes on downstream displacement of 12, 3 and 0 day-old brown trout (age after emergence) was investigated. Fish at each stage of development were introduced at hatching into distinct sections of two parallel artificial channels (experimental and control). Initially, the velocity was similar in both channels but in the experimental channel it was increased and then decreased between days $d = -1$ and $d = 2$, where $d = 0$ indicates the day on which the velocity reached its maximum value (Fig. 1). Channels were separated into four successive sections by traps. Three sections were used in each channel (those with the most homogeneous hydraulics). In the three sections, newly hatched brown trout were introduced at dates *c.* $d = -30$, $d = -20$ and $d = -16$. The dates were chosen as a function of temperature, with the objective that the three sections would contain 12, 3 and 0 day-old groups of brown trout (age after emergence) at $d = 0$. This experimental design was repeated in 2002 and 2003 at comparable dates, with $d = 0$ on 2 April 2002 and $d = 0$ on 29 March 2003 (see Table I for full details).

Artificial channels

Both channels had a length of 40 m and a slope of 0.5% (Fig. 2; Gaudin & Caillère, 1985). They were filled with gravel (1 to 5 cm size range). Natural food was available in



FIG. 1. Average water velocity (measured at 40% of total depth above the bed, every 10 cm, along three transects regularly spaced along each section) of the experimental channel from day $d = -1$ to day $d = 2$, where $d = 0$ is the day on which the velocity reached its maximum value. The date of the four-pass electrofishing of the channel (*i.e.* the end of the experiment) is given.

the channels. Ground water re-circulated by pumps, with a constant fresh supply of 1 l s^{-1} , was used. Water velocity was controlled by adjusting the discharge rate (pumps) into each channel.

For both 2002 and 2003, the mean \pm 95% CL width of sections was $0.94 \pm 0.01 \text{ m}$ (calculated from $n = 60$ regularly spaced measurements in the sections). During low-velocity periods, the mean \pm 95% CL velocity (at 40% of total depth above the bed and measured every 10 cm along three transects regularly spaced along each section) was $12.0 \pm 0.3 \text{ cm s}^{-1}$ ($n = 320$ measuring points) and mean \pm 95% CL depth (same measuring points) was $7.0 \pm 0.1 \text{ cm}$. For maximum velocity in the experimental channel, the mean \pm 95% CL velocity was $33.0 \pm 1.2 \text{ cm s}^{-1}$ ($n = 162$ measuring points) and the mean \pm 95% CL depth was $19.5 \pm 0.1 \text{ cm}$. Point velocities varied spatially across sections, especially in upstream parts of the sections but were well contrasted between low

TABLE I. Main characteristics of the experiments. d , number of days. Velocity was increased then decreased between $d = -1$ and $d = 2$ in the experimental channel. $d = 0$, the day on which the velocity reached its maximum value. The 0 d , 3 d and 12 d groups represented individuals that were 0, 3 and 12 days old (age after emergence) at $d = 0$

	First experiment	Second experiment
Date of introduction		
12 d group	$d = -29$	$d = -31$
3 d group	$d = -19$	$d = -21$
20 d group	$d = -15$	$d = -17$
Mean \pm 95% CL egg mass at eyeing (g)	0.0780 ± 0.0002	0.1020 ± 0.0004
Mean \pm 95% CL water temperature between $d = -1$ and $d = 2$ ($^{\circ} \text{C}$)	16.4 ± 0.1	16.2 ± 0.1

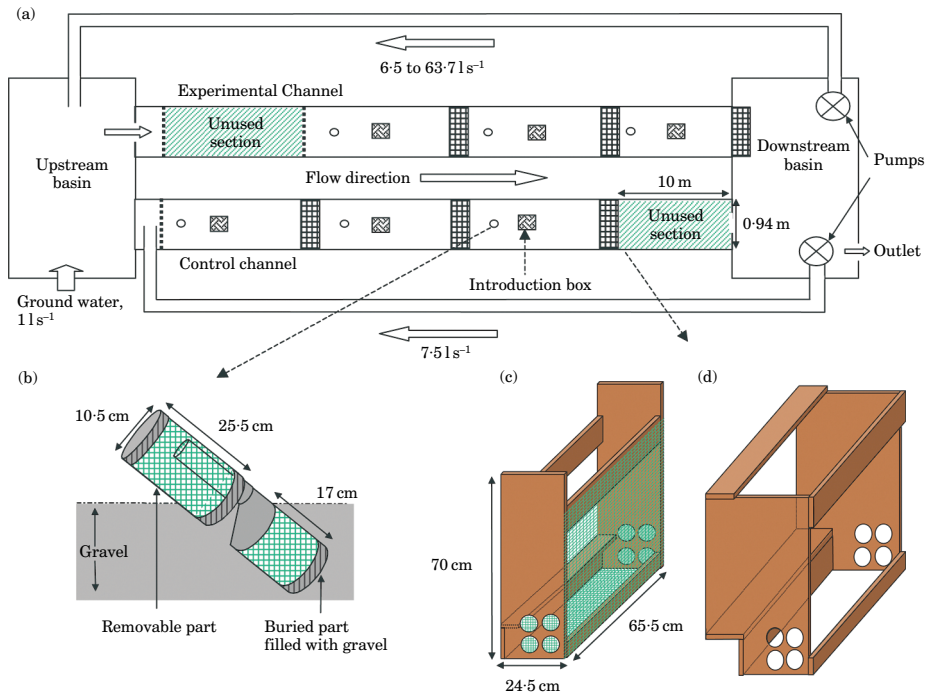


FIG. 2. (a) Schematic representation of the two artificial channels. Introduction box is the buried box ($30 \text{ cm wide} \times 30 \text{ cm long} \times 15 \text{ cm high}$, wire netting mesh = 2 mm) in which 250 fry were introduced at hatching. (b) Details of the emergence box (used to check for the timing of emergence of the fish) are given. (c) Removal trap and (d) fixed part of the dispersal trap are also shown.

and high velocity and comparable between years. The low velocity value corresponded to a low fish displacement rate (Ottaway & Clarke, 1981). The high velocity value matched observed values on spawning sites (Haury *et al.*, 1991), but such velocities were generally avoided by newly emerged fishes (Gaudin *et al.*, 1995; Heggenes *et al.*, 2002).

To control velocity change, before each experiment, additional measurements were taken in the experimental channel at velocities ranging from low to high. From $d = -1$, 0500 hours (solar time) to $d = -1$, 1900 hours, average velocity was increased every hour ($+1.5 \text{ cm s}^{-1} \text{ h}^{-1}$; Fig. 1). From $d = 0$, 2000 hours to $d = 2$, 2300 hours, average velocity was decreased every 2 hours [$-1.5 \text{ cm s}^{-1} (2 \text{ h})^{-1}$; Fig. 1].

Fish

Each of the groups of newly hatched brown trout introduced in the three sections of each channel (*c.* $d = -30$, $d = -20$ and $d = -16$, Table I) contained 250 individuals. They were all obtained from eggs of hatchery-reared wild fish. Progenitors were from the Furans River (69 km east of Lyon, France). All eggs were fertilized simultaneously following traditional methods and reared at 9° C until they became eyed. Eggs were then separated into three equal groups and incubated at 3° C . The incubation temperature of each group was then gradually increased to 12° C until hatching. The dates of the gradual warming of the incubation temperature of each group were adjusted to obtain the expected developmental stage at $d = 0$. Dates of emergence were predicted according to Crisp's (1992) equations (which provided an assessment of the brown trout development stage using mean daily temperatures) and from the fish farmer's experience for the Furans River stock. In each channel, the association between egg group and section was

random. Fish were introduced into the middle of the sections in a buried box (30 cm wide \times 30 cm long \times 15 cm high, wire netting mesh = 2 mm) filled with cleaned gravel.

Measuring the timing of emergence

In each section, 100 additional newly hatched fish (reared together with the other eggs) were introduced in closed emergence boxes, in order to check for the emergence dates of all groups [Fig. 2(b)]. The boxes, adapted from Gaudin & Persat (1985) were made of two connected cylinders: a buried part (10 cm in diameter \times 17 cm long, wire netting mesh = 2 mm) filled with cleaned gravel where the fish were placed; and an upper removable part (10 cm in diameter \times 25.5 cm long, wire netting mesh = 2 mm) in which fish were trapped as they emerged from the gravel. After the fish were introduced, the emergence boxes were checked each day at 1100 hours (solar time). At the end of the experiment ($d = 2, 11$ h), emergence boxes were emptied to evaluate fish loss.

Measuring the downstream displacement of fish

Experimental sections were separated by displacement traps [Fig. 2(c), (d)], used to collect fish moving downstream. They consisted of a fixed part receiving a removable trap. Two removal traps were made for each fixed part so that they could be replaced immediately when checked. Displacement traps were cleaned regularly to avoid blockage. From the first introduction on $d = -2$, displacement traps were checked every day at 1100 hours. Between $d = -1, 0500$ hours and $d = 2, 1100$ hours (solar time), the displacement traps were checked every 6 h (2300, 0500, 1100 and 1700 hours). This provided information on the influence of night on displacement rates. At the end of the experiment ($d = 2, 1100$ hours), all sections were electrofished with four passes to estimate the residual population in each section. Estimated efficiency of electrofishing ranged from 0.73 to 1 (Carle & Strube, 1978). At this efficiency rate, a four-pass electrofishing operation removes 99–100% of the population. In all cases, no fish were caught during the fourth pass. All fish trapped or electrofished were weighed.

STATISTICAL ANALYSIS

Total loss and emergence in boxes

The total loss in each emergence box was estimated as the difference between the initial number of fish introduced and the total number of fish emerged and recovered at $d = 2$.

The cumulative proportion of emerged fish in a box at sample i , E_i , was calculated as the ratio between the total number of emerged fish at sample i and the number of fish not lost before sample i . The number of fish not lost before sample i was obtained by summing the total number of emerged fish at sample i with the number of fish, not lost, remaining in the buried part of the box. This involved partitioning the total loss into instantaneous losses, as done by Crisp & Hurley (1991a): a constant loss rate was estimated that provided the observed total loss knowing the number of emerged fish at each sample; this estimation was obtained numerically using a simplex method.

Total loss and dispersion estimates in sections

The total loss in each section was estimated as the difference between the initial number of fish introduced and the total number of fish trapped and electrofished.

A cumulative displacement rate Cd_i was estimated as the ratio between the total number of fish displaced before sample i and the total number of fish not lost during the entire experiment.

For each section, the displacement rate at sample j , Γ_j , was calculated as the ratio between the number of fish trapped at sample j (n_j) and the number of emerged fish remaining in the section (not trapped before, not lost) at sample j . This again involved partitioning the total loss into instantaneous losses as done for the boxes. Finally, $\Gamma_j = n_j (S_j E_j)^{-1}$, where S_j is the potential number of fish remaining in the section at sample j (accounting for lost and trapped fish) and E_j is the cumulative proportion of emerged fish at sample j . E_j is derived from the relevant E_i value given by box samples, knowing that fish mainly emerge at night (Crisp, 1991; Bardonnnet *et al.*, 1993).

Analysis of Γ_j values between $d = -1$ and $d = 2$

For each group, the effects of velocity (average from hourly values between sample $j-1$ and j ; continuous variable) and night-time (2300 to 0500 hours; categorical variable) on Γ_j differences between the two channels (control and experimental) were tested using generalized linear models (GLM) (with an identity link function and a Gaussian dependent variable; McCullagh & Nelder, 1983). The dependent variable for these tests was the extra displacement rate R_j defined as:

$$R_j = (\Gamma_{\text{experimental},j} - \Gamma_{\text{control},j}) \left\{ \sqrt{p_j(1-p_j)[(S_{\text{experimental},j} E_{\text{experimental},j})^{-1} + (S_{\text{control},j} E_{\text{control},j})^{-1}]} \right\}^{-1},$$

with

$$p_j = (S_{\text{experimental},j} E_{\text{experimental},j} \Gamma_{\text{experimental},j} + S_{\text{control},j} E_{\text{control},j} \Gamma_{\text{control},j}) (S_{\text{experimental},j} E_{\text{experimental},j} + S_{\text{control},j} E_{\text{control},j})^{-1}.$$

R_j is the difference between Γ_j in the two channels, weighted by the number of emerged fish remaining in the sections. $R_j = 0$ when $\Gamma_{\text{experimental},j} = \Gamma_{\text{control},j}$. It is used in proportion comparison tests (Saporta, 1978) and accounts for non-equality in error rates.

To test for the accuracy of performing one model per group, a global model incorporating the velocity and night time as explanatory variables (model 1) was used. The fish group and the interactions between fish group and velocity and fish group and night-time as explanatory variables (model 2) were then added. The two models were compared using an analysis of deviance (McCullagh & Nelder, 1983). The difference between the residual deviances of two models is a χ^2 variable with n d.f. where n is the difference between the residual d.f. of the two models. This test checked whether the additional explanatory variables significantly decreased the residual deviance of the model.

Finally, to test the effect of the year (2002 or 2003; categorical variable) over all the experiments, a third model (model 3) was constructed, adding the year

and the interactions between fish group and year to the explanatory variables of model 2. Model 3 and model 2 were compared using an analysis of deviance.

The influence of a particular sample (j) on Γ_j differences was tested using χ^2 tests. Estimators of the number of emerged fish remaining in the sections, however, are not integer numbers. For a conservative solution, the estimators of the number of emerged fish remaining in the sections were rounded to the nearest higher integer for the experimental channel and to the lower integer for the control channel.

To check for the influence of the estimation method of S_j and E_j on the results, an analysis was also performed in which it was considered that all the fish were emerged at any sample j ($E_j = 1$) and that all the observed loss occurred when fish were introduced into the channels. S_j were thus calculated as the difference between the total number of fish recovered at the end of the experiment (trapped or electrofished) and the total number of fish displaced before sample j , as was done by Ottaway & Clarke (1981).

Finally, for each section, the mean masses of trapped fish were compared with the masses of fish electrofished at $d = 2$ using a standard t -test. All tests were performed using S-plus software (Mathsoft, 2000).

RESULTS

TOTAL LOSS (EMERGENCE BOXES AND SECTIONS)

The total loss was similar between emergence boxes and sections in 2002 (1.2–15.6%) (Table II). The losses were more variable and higher in 2003 (Table II). In particular, losses were 57.6% of the 0d-group fish in the control

TABLE II. Total loss rate observed in the emergence boxes and in the different channel sections for each group of brown trout (see Table I). Loss rates were the proportion of fry which were not recovered (*i.e.* not trapped and not electrofished). These proportions were calculated for each section as a proportion of the total number of fish introduced (*i.e.* 100 for the emergence boxes and 250 for the sections). The number of fish electrofished at the end of the experiment in each section are in parentheses. High loss rates are in bold

Year	Group		Emergence box (%)	Section (%)
2002	0d	Control channel	6.0	15.6 (106)
		Experimental channel	8.0	12.4 (82)
	3d	Control channel	4.0	6.7 (45)
		Experimental channel	5.0	15.2 (41)
	12d	Control channel	2.0	4.0 (45)
		Experimental channel	11.0	1.2 (41)
2003	0d	Control channel	99.0	57.6 (60)
		Experimental channel	21.0	5.2 (92)
	3d	Control channel	3.0	0.4 (53)
		Experimental channel	2.0	4.0 (48)
	12d	Control channel	2.0	5.9 (38)
		Experimental channel	0.0	26.3 (26)

section, 26.3% of the 12d-group fish in the experimental section, 21.0% of the 0d-group fish in the control emergence box and 99% of the 0d-group fish in the experimental emergence box (only one fish was recovered).

EMERGENCE IN BOXES

The E_i values revealed that the synchronization between emergence of the different fish groups and increased velocity periods was well controlled and similar for both experiments (Fig. 3).

In 2002, most of the 12d-group fish (55%) emerged in both channels at $d = -13$. Most of the 3d-group fish (62%) emerged in the experimental channel at $d = -3$. Half of the 3d-group fish (48%) emerged in the control channel at $d = -3$. Most of the 0d-group fish (64%) emerged in both channels at $d = 0$.

In 2003, most of the 12d-group fish (63%) emerged in both channels at $d = -12$. Half of the 3d-group fish (c. 50%) emerged in both channels at $d = -3$. Most of the 0d-group fish (58%) emerged in the experimental channel at $d = 0$.

CUMULATIVE DISPLACEMENT RATE IN SECTIONS

About 80% of the 12d-group fish were already trapped 5 to 6 days after median emergence ($d = -7$, Fig. 4) in both channels. The velocity increase did not modify the global displacement dynamics of this fish group.

Similarly, c. 80% of the 3d-group fish were trapped at the end of the experiment (5 days after median emergence) in both channels. The velocity increase in the experimental channel, however, slightly accelerated downstream displacement patterns (see Fig. 4).

In contrast, displacement of the 0d-group fish differed between channels, with an immediate, stronger downstream displacement in the experimental channel during velocity increase (Fig. 4).

ANALYSIS OF Γ_j VALUES BETWEEN $D = -1$ AND $D = 2$

Because of an exceptionally high loss rate of the 0d-group fish in the control emergence box in 2003, E_i values from the 0d-group in the experimental emergence box were used to calculate Γ_j values of the 0d-group in the control section.

The GLMs per group highlighted a positive effect of high water velocity and night-time on R_j values of the 0d-group and a positive effect of night-time on R_j values of the 3d-group (Table III and Fig. 5). Sample-specific tests indicated that the latter effect was due to a high displacement rate of the 3d-group in the experimental channel during the first night (Fig. 5) in 2002 (χ^2 test, d.f. = 1, $P < 0.01$ for both the 2300 and 0500 hour samples) and 2003 (χ^2 test, d.f. = 1, $P < 0.01$ for the 2300 hours sample). Nothing influenced the 12d-group displacement. The displacement rates of the 12d-group were low (close to 5%; Fig. 5) except in the experimental channel on $d = 0$ at 0500 hours in 2003 (χ^2 test, d.f. = 1, $P < 0.001$, $\Gamma_j = 14.7\%$). Additional explanatory variables of model 2 significantly decreased the deviance of the model compared to model 1 (χ^2 test, d.f. = 6, $P < 0.01$). Comparison of models 2 and 3 indicated that the year did not significantly influence the result (χ^2 test, d.f. = 3, $P > 0.05$).

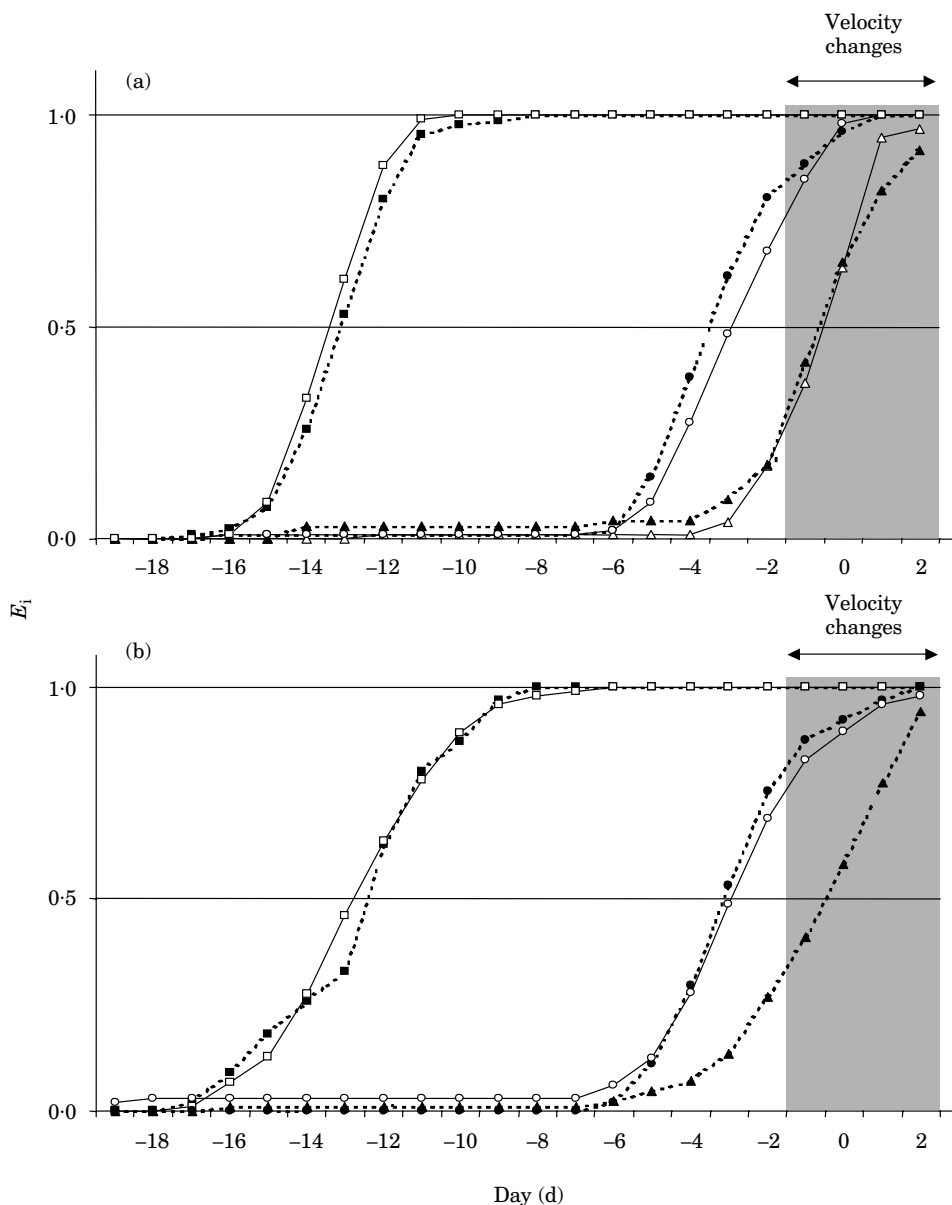


FIG. 3. Cumulative proportion of emerged fish (E_i) time series of the 12d-group in the control emergence box ($-\square-$), the 12d-group in the experimental emergence box ($--\blacksquare--$), the 3d-group in the control emergence box ($-\circ-$), the 3d-group in the experimental emergence box ($--\circ--$), the 0d-group in the control emergence box ($-\triangle-$) and the experimental emergence box ($--\blacktriangle--$) in (a) 2002 and (b) 2003. \blacksquare , the period during which the velocity was increased then decreased in the experimental channel. Because of a high loss rate, the time series for the cumulative proportion of emerged fish of the 0d-group in the control emergence box in 2003 is not represented. (See Table 1 for group definitions.)

All these results were similar considering that $E_j = 1$ for any sample j and calculating S_j , as was done by Ottaway & Clarke (1981).

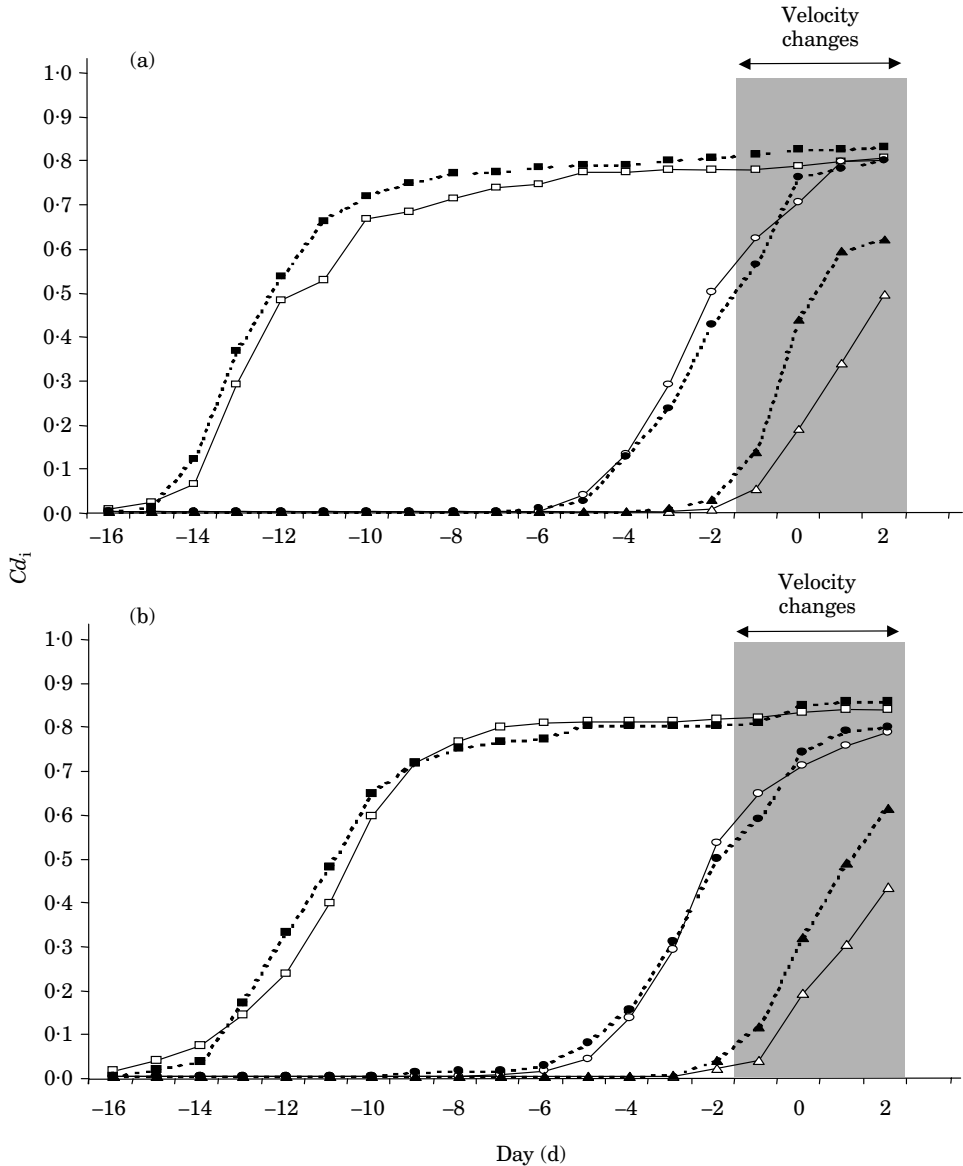


FIG. 4. Cumulative dispersal rate (Cd_i) of the 12d-group in the control channel (\square —), the 12d-group in the experimental channel (\blacksquare —), the 3d-group in the control channel (\circ —), the 3d-group in the experimental channel (\bullet —), the 0d-group in the control channel (\triangle —), the 0d-group in the experimental channel (\blacktriangle —) in (a) 2002 and (b) 2003. (See Table I for group definitions.)

In 2002 and 2003, the non-displaced fish (*i.e.* electrofished at $d = 2$) were significantly larger than the fish trapped between $d = -1$ and $d = 2$ in all sections (t -tests, d.f. = 34 to 210, $P < 0.01$). The mass difference appeared to be particularly pronounced for the 12d-group.

TABLE III. Results of the GLMs used on the extra dispersal rate R_j observed in the experimental channel between $d = -1$ and $d = 2$. (See Table I for group definitions)

Group		Value	S.E.	<i>t</i>	<i>P</i>
0d	Intercept	-1.86	0.76	-2.45	<0.05
	Velocity	10.33	2.92	3.54	<0.01
	Night-time	0.50	0.24	2.10	<0.05
(Residual deviance = 32.64 with 23 d.f.)					
3d	Intercept	-1.21	1.04	-1.16	>0.05
	Velocity	4.94	4.01	1.23	>0.05
	Night-time	0.87	0.33	2.69	<0.05
(Residual deviance = 61.62 with 23 d.f.)					
12d	Intercept	-0.40	0.53	-0.76	>0.05
	Velocity	1.73	2.05	0.85	>0.05
	Night-time	0.17	0.17	1.01	>0.05
(Residual deviance = 16.10 with 23 d.f.)					

DISCUSSION

The results suggest that young brown trout were highly sensitive to velocity changes during the first few days after emergence, especially during night-time. Occurring during emergence, velocity changes induced strong downstream displacement. The displacement patterns of the 3d-group indicated that this effect lasted until 80% of young brown trout had moved downstream. Once these thresholds had been reached, very few individuals were displaced downstream, independent of all water velocity treatment. Fish from the 3d-and 12d-groups reached the same thresholds under constant, low velocity conditions but the period of displacement was much more extended (5 to 6 days after emergence compared to 3 days after emergence under velocity changes). In this way, velocity changes advanced the time by which 80% of the fish moved downstream. The first days after emergence correspond to the acquisition of swimming capacity (Héland, 1991). Then fish establish territories up to about 12 days after emergence (Héland, 1991). The important mass differences between displaced and non-displaced 12d-group fish revealed that the displacement pattern was probably driven more by competition for space 12 days after emergence.

The results were highly consistent in 2002 and 2003. This showed that the variable loss rate observed between sections and between years did not influence the downstream displacement patterns. In addition, a large maternal size could be considered as a competitive advantage for salmonids because it is negatively related to the young fish mortality rate (Einum & Fleming, 2000). Larger egg size in 2003 (*i.e.* larger maternal sizes; Elliott, 1994) (Table I), however, did not influence displacement patterns. Finally, for both years, displacement patterns were highly consistent in the control channel for all three groups (especially for the 3d-and 12d-groups), indicating that the different incubation conditions did not influence the results.

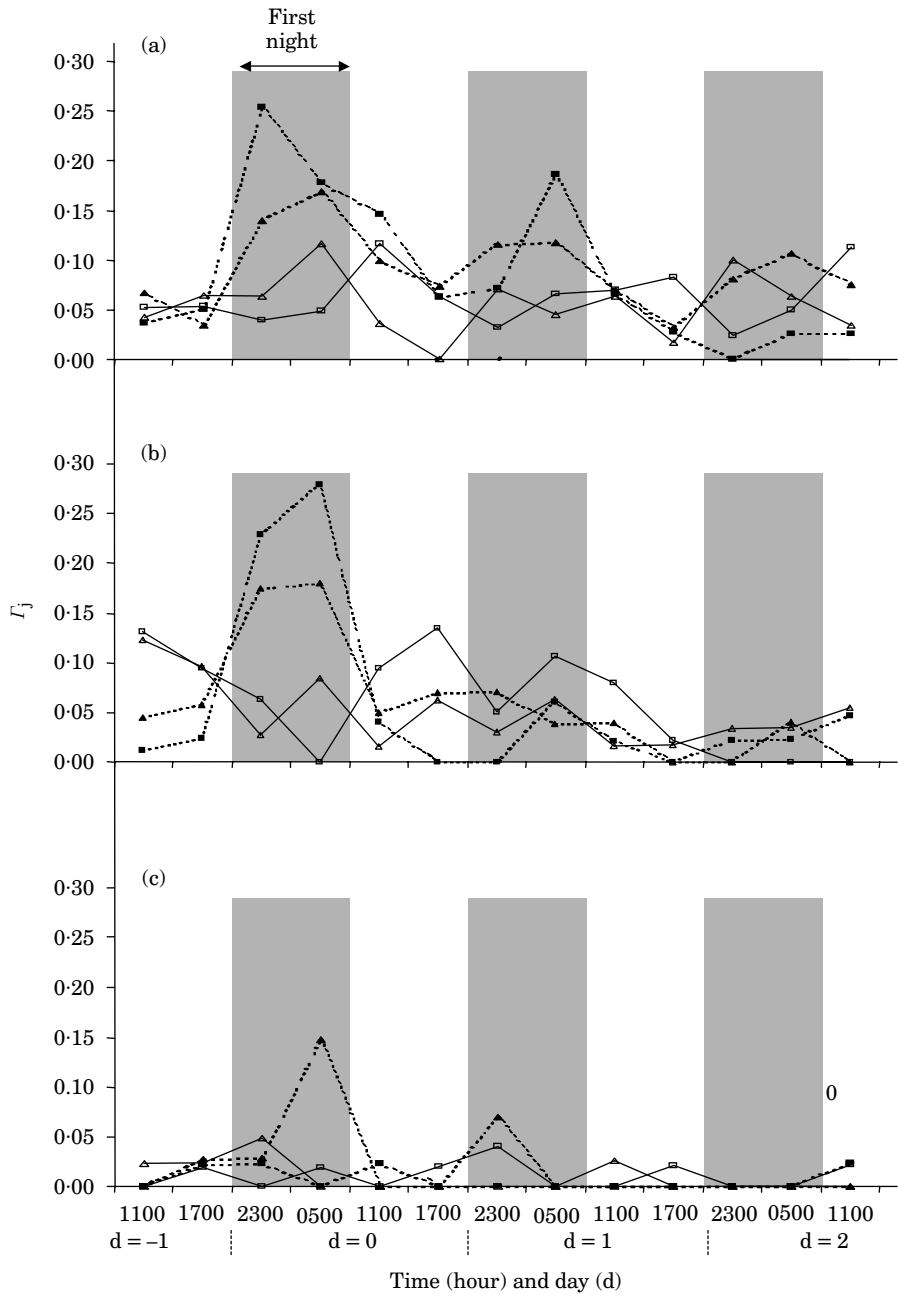


FIG. 5. Dispersal rate (Γ_j) of (a) 0d-, (b) 3d- and (c) 12d-group fish in the experimental channel in 2002 (---■---), the control channel in 2002 (—□—), the experimental channel in 2003 (---▲---) and the control channel in 2003 (—△—). ■, night-time. (See Table I for group definitions.)

Equal and high total rates of displacement (80%) for the 3d- and 12d-groups in all water velocity treatments were observed. This could mean that the low velocity (12.0 cm s^{-1}) was already too fast to be withstood by the fish. Newly

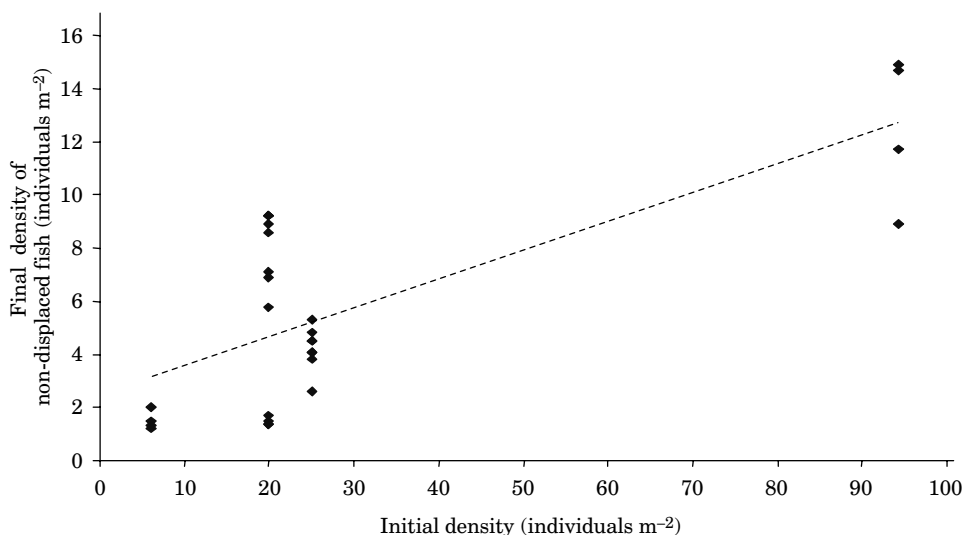


FIG. 6. Relationship between the initial density and the final density of non-dispersed fish in the present experiments (initial density = 25 individuals m^{-2}) and the experiments of Crisp (1991) and Crisp & Hurley (1991a, b). The trend curve (linear regression line) was fitted by $y = 0.11x + 2.5$. Final densities of non-dispersed 0d-group fish were not used to calculate the mean final density in the experiments.

emerged fish, however, naturally experience comparable velocities (Gaudin *et al.*, 1995) and roughness of the substratum probably allowed fish to shelter in 'dead' water zones (Crisp & Hurley, 1991a). In addition, greater displacement rates were observed at both lower and higher velocities (Ottaway & Clarke, 1981; Crisp & Hurley, 1991a), indicating that displacement could not be only attributed to swimming abilities (Crisp & Hurley, 1991a). Temperature could also influence fish swimming performance. Experiments were conducted, however, at water temperatures ($16.4^{\circ}C$ in 2002 and $16.2^{\circ}C$ in 2003) close to the optimal temperature for the swimming performance of young brown trout (*i.e.* optimal temperature $>12.4^{\circ}C$ for fish just after resorption of the yolk sac; Heggenes & Traaen, 1988; optimal temperature equal to $16.1^{\circ}C$ c. 4 months after the resorption of the yolk sac; Ojanguren & Brana, 2000). Finally, although the proportion of displaced fish seemed high, final densities (ranging from 2.6 to 5.3 individuals m^{-2} for the 3d- and 12d-groups) corresponded to densities observed in other experiments and in the field (Mortensen, 1977; Héland, 1980; Ottaway & Clarke, 1981; Ottaway & Forrest, 1983; Crisp, 1991; Crisp & Hurley, 1991a, b; Elliott, 1994).

In Crisp's (1991) experiments, similar final fish density was observed in channels submitted to different but constant velocities. This final density was approached more rapidly at high velocity. The present results, involving velocity changes, were consistent with these results. A constant final proportion of displaced fish (80%) but not a constant final density, however, was observed in the present experiments. For example, the final density of the 12d-group in the experimental channel was 4.1 and 2.6 individuals m^{-2} in 2002 and 2003,

respectively, because of different total loss rates. It is thus probably more accurate to consider that a velocity change advanced the attainment of the proportion of 80% of displaced fish rather than the attainment of a constant final density. This hypothesis is also supported by the relationship between initial and final densities observed in both the present and Crisp's (1991) experiments (Fig. 6). Despite very different durations and velocity treatments, initial and final densities seem positively linked.

The present results have shown that there is a short critical period during the early life history of brown trout. This period corresponds to the time it takes to reach a total rate of displaced fish close to 80%, that is to say the 5 to 6 day period after median emergence at constant low velocity (12 cm s^{-1}). During this period, it was surprising to observe a qualitative effect of velocity changes on the fry displacement pattern (velocity change advanced the attainment of a constant final proportion of displaced fish) consistent with Crisp's (1991) experiments. This makes it difficult to easily explain the link between displacement patterns and extra-mortality of YOY observed *in natura* under the high discharge condition during emergence (Allen, 1951; Nehring & Anderson, 1993; Nuhfer *et al.*, 1994; Latterell *et al.*, 1998; Liebig *et al.*, 1999). Environmental constraints associated with flood other than velocity (*e.g.* an increase in suspended matter) may hindered YOY survival. Since Héland (1980) showed that displaced fish are not necessarily moribund, studies focusing on the fate of displaced fish could also be of major interest for a full understanding of salmonid recruitment processes. The advance of fish downstream displacement under high water velocity could, for example, negatively influence their survival in downstream zones.

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