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Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress

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In non-drought years (1977, 1985), temperatures and oxygen concentrations from 1 to 14 July at the deepest point in each of five pools in Wilfin Beck were similar with ranges of 12–18° C and 7·8–9·8 mg l^{-1}. Trout *Salmo trutta* were present in all pools. In drought years (1976, 1983), temperature increased and oxygen concentration decreased as pool size decreased. In the two smallest pools, they were outside the thermal and oxygen limits for trout (ranges for both pools 24–29° C, 1·2–2·5 mg l^{-1}), and trout were absent. Values in a medium-sized pool were close to the incipient lethal levels and a few juvenile trout were present in both drought years. The lowest temperatures and highest oxygen concentrations were recorded in the two largest pools (ranges 20–25° C, 3·6–4·8 mg l^{-1}) and trout of all ages (0+ to adults) were present in both drought years. In these two pools, both temperature and oxygen concentration decreased from the surface to the deepest point in the pool. Trout preferred lower temperatures near the pool bottom rather than higher oxygen concentrations near the surface, but some fish moved towards the surface at night when the pool cooled slightly. These field results were discussed in relation to lethal values recorded for brown trout in the laboratory, and there was general agreement between field and laboratory values. Trout in the drought years occurred at temperatures close to, or below, the incipient lethal value of 24·7° C (±0·5) and also at the highest oxygen concentrations, but only when these were at temperatures below the incipient lethal value.

Key words: brown trout; droughts; environmental stress; oxygen; *Salmo trutta*; temperature.

INTRODUCTION

Severe droughts have marked effects on salmonid populations by reducing the volume of water available to the fish, impeding or preventing their migration and adversely affecting water quality, especially water temperature and dissolved oxygen. In a 30-year study (1966–1996) of a sea trout *Salmo trutta* L. population in Black Brows Beck, summer droughts led to increased mortality and decreased growth of the trout; the four most important droughts being, in order of severity: 1995 (most severe), 1976, 1983 and 1984 (Elliott *et al.*, 1997). The 1976 summer drought also caused high mortalities of adult salmon *Salmo salar* L. in the River Wye (Brooker *et al.*, 1977) and juvenile salmon in a small upper tributary of the River Severn (Cowx *et al.*, 1984). As Black Brows Beck rises from springs and peat moss in mixed woodland, most of the stream was never completely dry during the droughts except near the stream mouth. In contrast, the surface of the bed in the parent stream (Dale Park Beck) was completely dry, but a reduced

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flow continued within the bed. The same occurred in many neighbouring streams and trout were found only in isolated pools.

One of these streams was Wilfin Beck, which has a population of resident brown trout living above an impassable waterfall (Elliott, 1994). An October census in this stream from 1965 to 1983 was used to develop population models so that observed densities of trout could be compared with values predicted from the models (Elliott & Hurley, 1998). There was generally good agreement between observed values and those expected from the models, except in summer droughts. Two such droughts occurred in 1976 and 1983, and observed densities in October were much lower than expected for 0+ and 1+ trout, but not for 2+ and older fish. Pools were used as refugia by the trout during each drought.

The chief objective of the present study was to examine some characteristics of these pools in the two drought years (1976, 1983), especially in relation to the trout responses to thermal and oxygen stress, and to compare these characteristics with those found in the same pools in two non-drought years (1977, 1985).

MATERIALS AND METHODS

GENERAL STUDY OF FIVE POOLS

Wilfin Beck is situated in north-west England in the southern part of the English Lake District, and flows into Windermere. As the stream was described in detail by Elliott (1973, 1987, 1994), only a brief summary is provided here. The stream is *c.* 4 km long and a waterfall, that is impassable to upstream migrating trout, occurs *c.* 800 m from the stream mouth. The stream above the waterfall is populated by only resident brown trout that live chiefly in the upper 2 km where the five sampling sites for the October census were situated (see Fig. 1 in Elliott, 1987). The five pools in the present study were all within or near these sites. Two pools were chosen because they were the largest in the stream, but the other three were chosen at random from a larger number of smaller pools.

Some characteristics of the pools were recorded every day from 1–14 July in the two drought years (1976, 1983) and in two non-drought years (1977, 1985). Ideally, the non-drought years should have been the next year after the drought year, but this was impossible in 1984 because this was also a drought year. Surface area and maximum depth were measured daily to the nearest m^2 and 0·05 m respectively. A maximum and minimum, mercury in glass, thermometer was placed at the deepest point in each pool, and read and reset daily at about midday, measurement being to the nearest 0·5° C. Each thermometer was in a heavy-metal tube so that it was not exposed to direct sunlight. Oxygen concentration was measured daily (to nearest 0·1 mg l^{-1}) at the deepest point in each pool at midday and midnight (Greenwich Mean Time: GMT), using a Mackereth (1964) oxygen meter. Finally, the presence or absence of trout was recorded. The trout were separated into adults and juveniles, and the latter were aged from their size. The standard convention for aging was followed: 0+ trout were <1 year old, 1+ trout were between 1 and 2 years old, 2+ trout were between 2 and 3 years old, and adults were >3 years old.

DETAILED STUDY OF TWO POOLS

The characteristics of the two deepest pools were examined in more detail over 4 days (midday on 11 July to midday on 14 July) in each of the four years. The oxygen meter also measured temperature and was used to take simultaneous readings of water temperature (to nearest 0·1° C) and oxygen concentration (to nearest 0·1 mg l^{-1}) every 2 h (n=37) at the following depths in each pool: 0·10 m (near surface), 0·50 m, 1·00 m and at the deepest point in the pool (1·45 m in 1976, 1·50 m in 1983, 1·65 m in 1977 and 1985 for pool 1; 1·35 m in 1976 and 1983, 1·45 m in 1977 and 1985 for pool 2). A rod marked at 0·5 m and 1·0 m was placed at the deepest point in each pool and was used to estimate the vertical distribution of the trout at midday and midnight (GMT). As the two pools were some distance apart, observations in pool 2 were made about 5 min after those in pool 1. Counts were made of the trout present in three layers: surface to 0·5 m, 0·5 to 1·0 m, and 1·0 m to pool bottom. A red light was used to observe the trout at midnight. As there were few trout in each pool, it was possible to estimate the age of the fish in each layer (0+, 1+, 2+ and adults) from their size.

RESULTS

GENERAL STUDY OF FIVE POOLS

The five pools had surface areas in the range 2–25 m^2 and maximum depths in the range 0·4–1·65 m (Table I). Surface area and maximum depth remained constant for each pool in the non-drought years (1977, 1985), but both decreased slightly over the study period (1–14 July) in the drought years (1976, 1983). Maximum and minimum temperatures at the deepest point were similar among the five pools in the non-drought years with mean maximum values of 17·0° C in 1977 and 15·0–15·5° C in 1985, and mean minimum values of 15·0° C in 1977 and 12·0° C in 1985.

In drought years, temperatures at the deepest point varied considerably between pools and increased markedly as pool size decreased (Table I). There was a significant (P<0·001) negative correlation between maximum depth and both mean maximum ($r = -0{\cdot}986$) and mean minimum ($r = -0{\cdot}970$) temperatures. Pools 4 and 5 had the highest temperatures with maximum values in the ranges 26–29° C in 1976 and 26–28° C in 1983, and minimum values in the range 24–26° C in both years. These values exceeded the incipient lethal temperature for brown trout in the laboratory. Trout were absent from both pools in the drought years, whereas 1+ trout were found in the smaller pool 5, and 1+ and 2+ trout in the slightly larger pool 4 in the non-drought years. Trout aged 1+ and 2+ were also found in pool 3 in the non-drought years, but only three 0+, and two 0+ with two 1+, trout were found in the drought years of 1976 and 1983 respectively. Temperatures in pool 3 were close to the incipient lethal value for brown trout. Although temperatures in pools 1 and 2 were much higher in drought years than in non-drought years, they were the lowest recorded in the five pools and were always below the incipient lethal value with maximum and minimum values in the ranges 23–25 and 20–23° C respectively. Trout of all age groups from 0+ to adults were found in pools 1 and 2 during the summer droughts, but only older trout (2+, adults) were present in the non-drought years.

The patterns shown by oxygen concentrations measured at the deepest point at midday and midnight (GMT) were related to those for temperature (Table I). Values were similar among the five pools in the non-drought years (1977, 1985), but midnight values were always slightly lower than midday values with overall ranges for all pools of 7·8–9·4 mg l^{-1} for midnight and 8·8–9·8 mg l^{-1} for midday. These values were equivalent to % air saturation values (% ASV) above 76%, with most values over 90%, and therefore ideal for trout. In contrast, oxygen concentration varied considerably between pools in the drought years (1976, 1983) and decreased as pool size decreased (Table I). There was a significant (P<0·001) positive correlation between maximum depth and both

TABLE I. Some characteristics of five pools sampled in two drought years (1976, 1983) and two non–drought years (1977, 1985); mean values (with ranges in parentheses) were for daily readings from 1 to 14 July in each year; presence of trout indicated by age groups (0+, 1+, 2+, adults) found in each pool; pools ranked from largest to smallest (note that temperature and oxygen concentration were recorded only at the deepest point in each pool)

Pool	Surface area (m^2)	Max. depth (m)	Max. temp. (° C)	Min. temp. (° C)	Midday O_2 ($mg\ l^{-1}$)	Midnight O_2 ($mg\ l^{-1}$)	Trout (ages)
1: 1976	24 (23–25)	1·55 (1·45–1·65)	23·5 (23·0–24·0)	22·0 (22·0–22·0)	4·3 (3·8–4·8)	4·1 (3·6–4·6)	0+, 1+, 2+, A
1983	24 (23–25)	1·55 (1·50–1·65)	23·0 (22·5–23·5)	21·5 (21·0–22·0)	4·4 (4·1–4·7)	4·3 (4·0–4·6)	0+, 1+, 2+, A
1977	25 (25–25)	1·65 (1·65–1·65)	17·0 (16·0–18·0)	15·0 (14·0–16·0)	9·1 (8·8–9·4)	8·1 (7·8–8·4)	2+, A
1985	25 (25–25)	1·65 (1·65–1·65)	15·5 (14·0–17·0)	12·0 (12·0–12·0)	9·1 (8·9–9·3)	8·6 (8·2–9·0)	2+, A
2: 1976	12 (11–13)	1·40 (1·35–1·45)	24·0 (23·0–25·0)	22·0 (21·0–23·0)	4·2 (3·8–4·6)	4·1(3·7–4·5)	0+, 1+, 2+, A
1983	12 (11–13)	1·40 (1·35–1·45)	23·5 (23·0–24·0)	21·0 (20·0–22·0)	4·4 (4·0–4·8)	4·2 (3·9–4·5)	0+, 1+, 2+, A
1977	13 (13–13)	1·45 (1·45–1·45)	17·0 (16·0–18·0)	15·0 (15·0–15·0)	9·2 (8·8–9·6)	8·2 (8·0–8·4)	2+, A
1985	13 (13–13)	1·45 (1·45–1·45)	15·5 (14·0–17·0)	12·0 (12·0–12·0)	9·3 (8·8–9·8)	8·6 (8·3–8·9)	2+, A
3: 1976	7 (4–8)	0·75 (0·50–0·85)	26·0 (25·0–27·0)	24·5 (23·5–25·5)	2·8 (2·5–3·1)	2·2 (2·0–2·4)	0+
1983	7 (4–8)	0·80 (0·55–0·90)	26·0 (25·0–27·0)	24·0 (23·0–25·0)	2·9 (2·4–3·4)	2·3 (2·0–2·6)	0+, 1+
1977	8 (8–8)	0·90 (0·90–0·90)	17·0 (16·0–18·0)	15·0 (15·0–15·0)	9·4 (9·2–9·6)	9·0 (8·7–9·3)	1+, 2+
1985	8 (8–8)	0·90 (0·90–0·90)	15·0 (14·0–16·0)	12·0 (12·0–12·0)	9·2 (9·0–9·4)	8·8 (8·5–9·1)	1+, 2+
4: 1976	4 (2–5)	0·60 (0·45–0·75)	27·5 (26·0–29·0)	25·0 (24·0–26·0)	2·1 (2·0–2·2)	1·6 (1·2–2·0)	None
1983	4 (2–5)	0·65 (0·50–0·80)	27·0 (26·0–28·0)	25·0 (24·0–26·0)	2·3 (2·1–2·5)	1·6 (1·4–1·8)	None
1977	5 (5–5)	0·85 (0·85–0·85)	17·0 (16·0–18·0)	15·0 (15·0–15·0)	9·5 (9·3–9·7)	9·0 (8·8–9·2)	1+, 2+
1985	5 (5–5)	0·85 (0·85–0·85)	15·0 (14·0–16·0)	12·0 (12·0–12·0)	9·3 (9·0–9·6)	8·9 (8·5–9·3)	1+, 2+
5: 1976	3 (2–4)	0·50 (0·40–0·55)	27·5 (26·0–29·0)	25·0 (23·5–26·5)	2·1 (2·0–2·2)	1·5 (1·3–1·7)	None
1983	3 (2–4)	0·55 (0·40–0·60)	27·0 (26·0–28·0)	25·0 (24·0–26·0)	2·2 (2·0–2·4)	1·7 (1·5–1·9)	None
1977	4 (4–4)	0·65 (0·65–0·65)	17·0 (16·0–18·0)	15·0 (15·0–15·0)	9·5 (9·2–9·8)	9·0 (8·6–9·4)	1+
1985	4 (4–4)	0·65 (0·65–0·65)	15·0 (14·0–16·0)	12·0 (12·0–12·0)	9·2 (8·8–9·6)	8·8 (8·3–9·3)	1+

midday (r=0·989) and midnight (r=0·983) mean oxygen concentrations. Values were lowest in pools 4 and 5 with mean values of $\leq$2·3 mg l^{-1} at midday and $\leq$1·7 mg l^{-1} at midnight. No values exceeded 30% ASV, most were <25% ASV, and trout were absent from both pools. Oxygen concentration in pool 3 in the drought years varied from 2·0–3·1 mg l^{-1} in 1976 and 2·0–3·4 mg l^{-1} in 1983. These values were equivalent to 24–39 and 23–43% ASV, respectively and were probably close to the lower tolerance limits for juvenile brown trout. Oxygen concentrations in pools 1 and 2 in the drought years were about half those in the non-drought years (Table I). Values varied from 3·6 to 4·8 mg l^{-1} in 1976 and 3·9 to 4·8 mg l^{-1} in 1983, these values being equivalent to 41–57 and 43–57% ASV respectively. These values were higher than incipient lethal values estimated from laboratory experiments.

DETAILED STUDY OF TWO POOLS

The relationships between mean temperatures or mean oxygen concentrations and water depth were similar for pools 1 and 2 in the two non-drought years (1977 ND and 1985 ND in Fig. 1). As depth increased, there were no significant differences in mean values [P>0·05 from one-way analysis of variance (ANOVA)]. Overall means were 15·9° C and 8·7 mg l^{-1} in 1977, 14·7° C and 8·9 mg l^{-1} in 1985 for pool 1 [Fig. 1(a), (b)], 16·1° C and 8·8 mg l^{-1} in 1977, 15·0° C and 9·0 mg l^{-1} in 1985 for pool 2 [Fig. 1(c), (d)]. Only older trout were present (Table I) with two adults and four 2+ trout in pool 1 in both years, and one adult in pool 2 in both years with two 2+ trout in 1977 and three 2+ trout in 1985. As the trout moved frequently from the bottom to the surface of each pool, it was impossible to record the number of fish present in the three depth layers.

In the two drought years (1976 D and 1983 D in Fig. 1), mean temperatures and mean oxygen concentrations both decreased significantly with pool depth (P<0·01 from one-way ANOVA). In pool 1, they decreased from 26·0 to 22·8° C and 4·8 to 4·1 mg l^{-1} in 1976, and from 25·6 to 22·4° C and 5·1 to 4·3 mg l^{-1} in 1983 [Fig. 1(a) and (b)]. In pool 2, they decreased from 26·0 to 23·1° C and 4·8 to 4·2 mg l^{-1} in 1976, and from 25·0 to 22·1° C and 4·8 to 4·4 mg l^{-1} in 1983 [Fig. 1(c) and (d)]. The oxygen values were about half those recorded at all depths in the non-drought years. The variation in both temperature and oxygen concentration was usually less in the drought years than in the non-drought years (cf. ranges in Fig. 1).

The distribution of the trout with depth in each pool showed a consistent pattern in the two drought years (Fig. 2). In pool 1, all 24 trout in 1976 and 22 trout in 1983 were only in the bottom layer (1·0 m—maximum depth) at midday [Fig. 2(a) and (b)]. Temperatures were *c.* 2° C lower by midnight and most trout were in midwater (0·5–1 m) with a few fish in the surface layer (0–0·5 m) in 1983 but not 1976. Only small trout (0+, 1+) remained near the bottom at midnight. In the smaller pool 2, all 13 trout were in the bottom layer at midday in 1976, but the ten trout recorded in 1983 were in the bottom and middle layers at midday [Fig. 2(c) and (d)]. At midnight, temperatures also decreased in this pool by about 2° C and trout occurred at all depths, with most fish in midwater.

There was a clear difference between temperatures for the depth layers with (●) and without (○) trout (Fig. 3). When trout were present, the mean

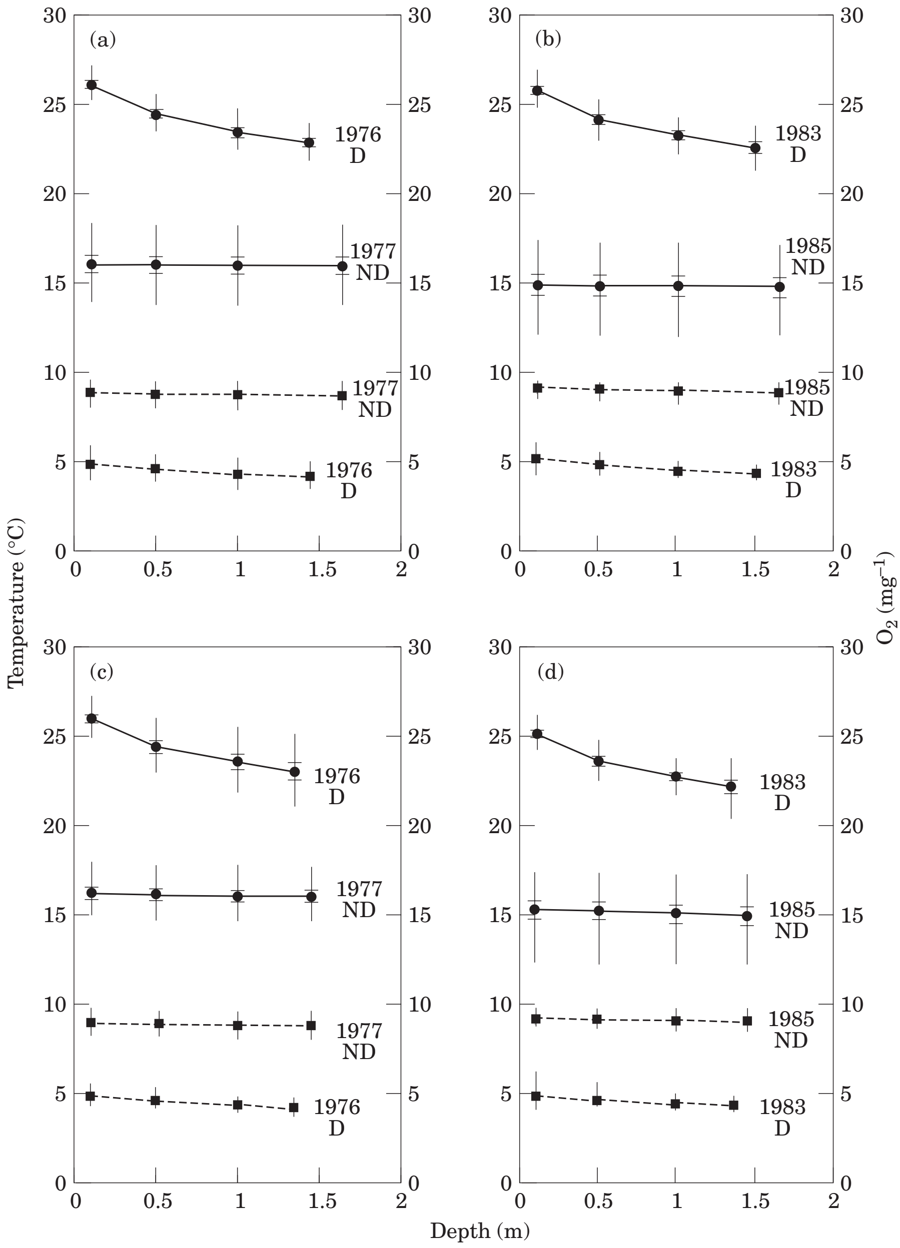

FIG. 1. Relationship between mean temperature (●) or mean oxygen concentration (■) and water depth in drought (D) and non-drought (ND) years; 95% CL and ranges (n=37) are given for temperature but only ranges for oxygen concentration (95% CL were too narrow to be shown). (a) Pool 1 in 1976, 1977; (b) pool 1 in 1983, 1985; (c) pool 2 in 1976, 1977; (d) pool 2 in 1983, 1985.

temperature was less than the incipient lethal level of 24·7° C (95% CL ± 0·5). The sole exception was a value of 24·9° C, which was still within the 95% CL of the incipient lethal value, and was recorded at the bottom of pool 2 at midday in

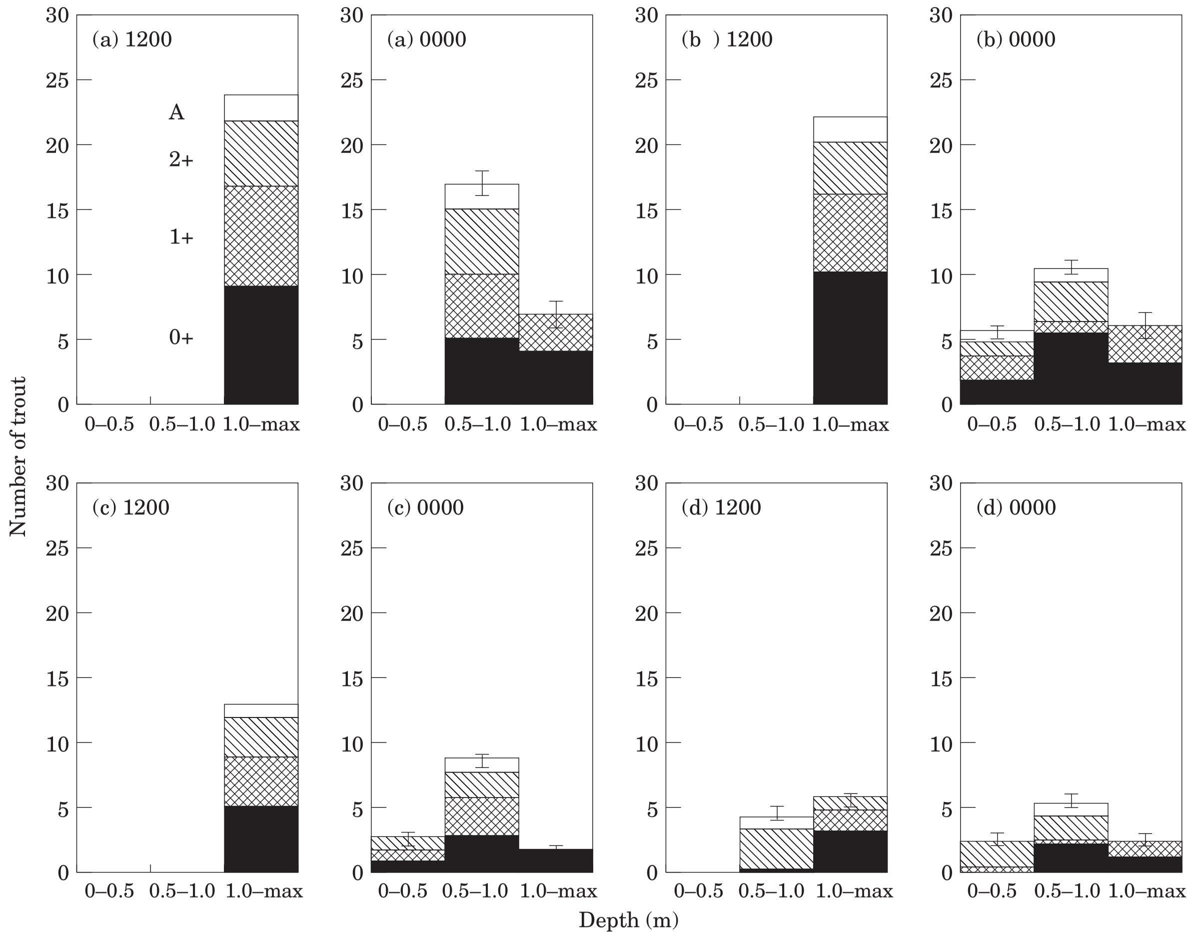

FIG. 2. Mean number of trout in three depth layers (0–0·5 m, 0·5–1·0 m, 1·0 m maximum depth) at midday (1200 hours) and midnight (0000 hours) with ranges for mean total numbers for each depth layer (vertical line); the number of trout in each age group is also shown for each depth layer (0+, 1+, 2+, adults: key in top left figure). (a) Pool 1 in 1976; (b) pool 1 in 1983; (c) pool 2 in 1976; (d) pool 2 in 1983.

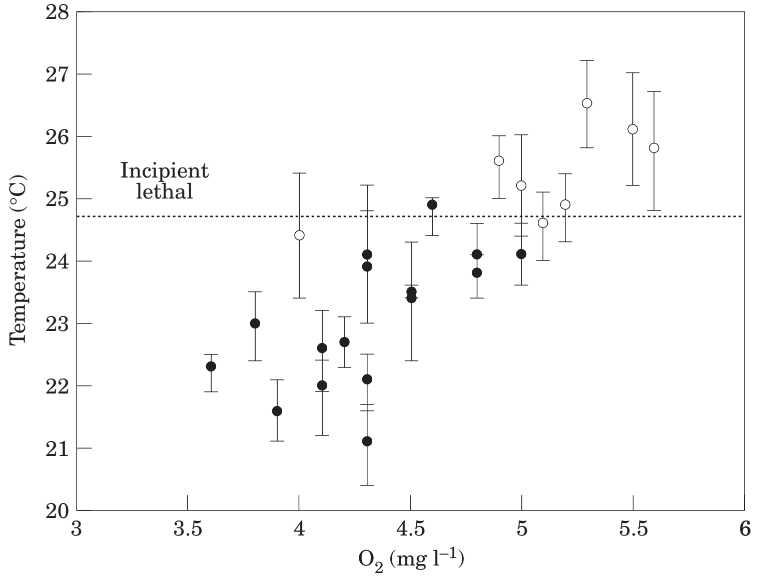

FIG. 3. Mean temperature (with range as vertical line) and mean oxygen concentration in each depth layer with (●) and without (○) trout present; horizontal broken line is the incipient lethal temperature of 24·7° C (95% CL ± 0·5) (from Elliott, 1981).

1976, so that the trout had no opportunity to move into cooler water. By midnight, however, temperatures from surface to bottom were all below the incipient lethal level and trout occurred in all three layers [Fig. 2(c)]. When trout were absent, temperatures were close to, or above, the incipient lethal value. Oxygen concentrations were usually higher in the depth layers without trout than in those with trout (Fig. 3). These comparisons and those for the depth distribution of trout in each pool (Fig. 2), showed clearly that when trout were faced with a choice of higher temperatures with higher oxygen concentrations, or lower temperatures with lower oxygen concentrations, they showed a preference for the latter combination.

DISCUSSION

Summer droughts are a regular feature of most trout streams but their severity varies considerably. Severe droughts reduce the volume of water available to trout and thereby force them into pools. It is difficult to separate the direct effects of a drought in a hot summer from the effects of high air temperatures, but the end result is that the fish have to cope with adverse water quality, especially increasing water temperature and decreasing oxygen concentration. The droughts of 1976, 1983, 1984 and 1995 increased mortality and decreased growth of juvenile sea trout in Black Brows Beck, but the effects were never catastrophic because the stream continued to flow at a low rate (Elliott *et al.*, 1997). In contrast, mass mortalities of salmon occurred in the River Wye during the summer drought of 1976 when minimum oxygen concentrations fell over 5 days from 5 to almost 1 mg l^{-1}, whilst maximum and minimum temperatures increased from 23 to 27·6° C and 21 to 25·2° C respectively (Brooker *et al.*, 1977). High mortalities of salmon and trout have been recorded in Norwegian rivers when oxygen concentrations fell below 2–3 mg l^{-1} (Bergheim *et al.*, 1976). Losses were also high in Wilfin Beck during summer droughts and were the result of high mortality rather than emigration from the stream (Elliott, 1994; Elliott & Hurley, 1998). There was little movement of trout within the stream, except by adults at spawning time and when trout moved into deeper pools during droughts (Elliott, 1987).

When streams dry up during severe summer droughts, pools are essential for salmonid survival, but the present study has shown that not all pools serve as refugia. Small pools that contain trout in non-drought years are devoid of trout during droughts when temperatures are too high and oxygen concentrations too low for the trout to survive, e.g. pools 4 and 5. Even in the larger pools serving as refugia, the trout do not occur at all depths but show a preference for the cooler water near the bottom, even though oxygen concentration is lower than that near the surface, e.g. pools 1 and 2. Therefore, survival depends upon suitable temperature and oxygen concentrations being available in each pool, and the trout respond to the thermal and oxygen stress.

The incipient lethal temperature is usually defined as that which fish (usually 50% of sample) can tolerate for a long period (7 days is usual standard) but beyond which fish cannot survive for an indefinite period (Elliott, 1994). The ultimate lethal temperature is that which fish cannot tolerate for a short period (10 min is usual standard). In a detailed study with brown trout in the laboratory, the incipient lethal temperature increased with increasing acclimation temperature to a plateau at 24·7° C (95% CL ± 0·5) while the ultimate lethal temperature reached a plateau at 29·7° C (± 0·36) (Elliott, 1981). Further experiments to determine the critical thermal maximum for brown trout produced similar values (Elliott & Elliott, 1995).

Temperatures in the two smallest pools, 4 and 5, were often higher than the incipient lethal level and sometimes close to the ultimate lethal level during the two droughts (Table I). No trout could tolerate such thermal stress. Temperatures in the intermediate-sized pool 3 in the drought years were well below the ultimate lethal value but exceeded the incipient lethal value for part of each day, usually from midday to early evening. The trout must have been subject to thermal stress during this period of the day. In the larger pools 4 and 5, trout were presented with a choice of temperatures during the two droughts (Fig. 1). They always showed a preference for temperatures below the incipient lethal value (Figs 2 and 3). These temperatures usually occurred near the bottom of the pool at midday, but were often found at all depths by midnight. Therefore, the position of the trout changed in response to the degree of thermal stress.

Opinions differ on the critical values of dissolved oxygen concentration for trout. Mills (1971) proposed a minimum concentration of 5·0–5·5 mg l^{-1} for brown trout to continue swimming in open water. This range was greatly exceeded in all the pools during the non-drought years (Table I, Fig. 1). It was rarely attained during the drought years and then only in surface waters from which trout were absent because of high temperatures (Fig. 3). Burdick *et al.* (1954) found that the ultimate lethal oxygen concentration for brown trout in the laboratory varied from 1·4 mg l^{-1} at 9° C to 2·5 mg l^{-1} at 21° C. The latter value was clearly more appropriate to the present study because of the high temperatures. It was never exceeded in drought years at the deepest point in the two smallest pools with no trout (pools 4 and 5 in Table I), and was not always exceeded in the intermediate pool 3 with a few small trout. These trout must have been subject to oxygen stress as well as thermal stress for part of each day. Most workers agree that the incipient lethal oxygen concentration for juvenile trout in the laboratory varies in the range 3–4 mg l^{-1} depending upon the temperature (Doudoroff & Shumway, 1967, 1970; Davis, 1975; Alabaster & Lloyd, 1982). In the deeper pools 4 and 5, the lower value in this range was always exceeded in drought years and the upper value was exceeded in most of the depth layers with trout present (Fig. 3). The overall range of oxygen concentrations experienced by the trout was 3·5–5·4 mg l^{-1}, and therefore there was general agreement between field and laboratory values.

Perhaps the most intriguing finding of the present study is that the trout showed clear preferences for certain combinations of temperature and oxygen concentration. They always chose depth layers in pools 4 and 5 where temperatures were close to, or below, the incipient lethal value of 24·7° C ($\pm$ 0·5). This often confined the trout to the deepest part of the pool (Fig. 2), even though oxygen concentrations were lowest in this layer (Fig. 1). When temperatures fell below the incipient lethal value in the middle and surface layers of each pool, the trout moved away from the bottom and were able to utilize the higher oxygen concentrations (Fig. 2). However, they never showed a preference for the highest oxygen concentrations when these occurred at temperatures above the incipient lethal value (Fig. 3). Similar results were obtained in a detailed study of the responses of rainbow trout *Oncorhynchus mykiss* (Walbaum) to temperature and oxygen concentration in two stream pools in southern California (Matthews & Berg, 1997). Most rainbow trout were found near the bottom at temperatures in the range 17·5–21° C and oxygen concentrations in the daily range 1–5 mg l^{-1} and the trout avoided the warmer surface waters with oxygen values of 4–10 mg l^{-1}. In both these studies, the two species of trout showed a similar behavioural response to thermal and oxygen stress and always chose low water temperatures near the pool bottom, even though oxygen concentrations were lower than those in the warmer surface waters. Such behavioural responses are clearly important factors for trout survival during severe droughts and the provision of suitable deep pools as refugia should be an essential part of a strategy for successfully managing trout populations. This was recognized by Reeves *et al.* (1991) in their extensive review of techniques for rehabilitating and modifying salmonid habitats. They summarized several successful case studies in which an increase in the number, size and depth of pools led to an increased abundance of fish, especially in streams subjected to frequent droughts. The pools also served as winter habitat, and provided refugia during periods of high flow. This review advocates the creation of refuge pools in salmonid streams, and the present study provides strong support for such a management strategy.

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